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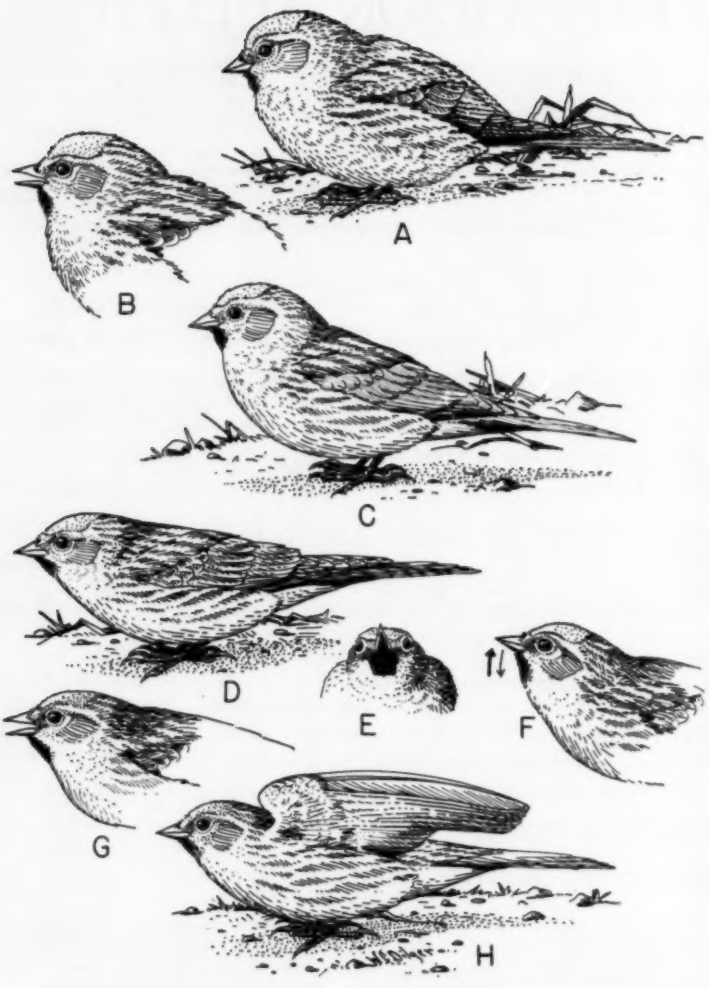

Postures of Redpolls: (A) Submissive display, (B) Defensive Threat, (C) normal relaxed posture, (D) basic Head Forward Threat display, (E) Head Forward Threat with Chin-lifting (front), (F) Head Forward Threat with Chin-lifting (side), (G) Head Forward Threat with Gaping, and (H) Head Forward Threat with Wings-raised (high intensity).

AGONISTIC AND SOCIAL BEHAVIOR OF CAPTIVE REDPOLLS

BY WILLIAM C. DILGER

THE birds used in this study were trapped on the campus of St. Lawrence University, Canton, New York, during February and March of 1956. A simple droptrap operated manually by means of a long cord was used, and a mixture of canary and rape seed served as bait. After two or three birds were caught and placed in a small cage next to the trap little difficulty was experienced in quickly obtaining others. Deep snow throughout the trapping period seemed to facilitate the trapping, as food was presumably difficult to procure elsewhere.

The objectives of this study were as follows: (1) to describe and evaluate the agonistic (attack-escape) behavior; (2) to describe and evaluate any social hierarchy that might be established; and (3) to obtain information on the changes in behavior associated with the gradual onset of reproductive condition during the spring.

Thirty-one Common Redpolls (*Acanthis flammea*) were used as a source of observational data, but only eight of these were studied intensively. The others provided subsidiary data as did the wild ones which remained in the vicinity. All captives were color-banded to facilitate the ready recognition of individuals. The group of eight was placed in a semi-box type cage measuring 3 feet by 2 feet by 2 feet high. The back, sides, and bottom were fashioned of plywood. The top was covered with ½-inch mesh screening and the front was constructed of glass in order to increase visibility into the interior. A sliding metal tray on the bottom facilitated cleaning the cage. The substrate consisted of paper over which a thin layer of coarse quartz sand was spread. Two perches running from front to back were fastened to the back of the cage about 6 inches from the floor and about 13 inches apart. A third perch, running parallel to the cage front, was fastened to the cage sides about 18 inches from the bottom and about a foot from the back.

Food consisted of a standard canary mixture (three parts canary and one part rape seed). In addition, small amounts of parakeet conditioning food were supplied. This consisted of a mixture of small seeds and a mash made up of milk proteins, dried egg yolk, ground oyster shells, vitamin supplements, etc. Fresh water and cuttle bone were continually available. Food and water were placed in steep-sided glass dishes about 4 inches in diameter and 1½ inches deep.

Close observation was made easier by the quickness with which they became habituated (a learning process characterized by a waning of a response despite repeated stimulation but not associated with any reinforcement . . . see Thorpe (1951) for a thorough discussion) to the cages and to human pres-

ence. As a matter of fact, it was not unusual for freshly caught birds to feed in the gathering cages as they were being carried from the trap to the laboratory! Once established in the observation cages they soon permitted observations to be made at a distance of 3 or 4 feet without the slightest apparent alarm.

The methods used to determine the function ("meaning" to other individual(s)) and stimulus strength of each of the displays discussed are those ordinarily used by ethologists and frequently discussed in the literature; for instance, Moynihan (1955*a*) and Hinde (1955–56). In brief, four types of evidence are utilized: (1) the circumstance in which the display occurs; (2) the behavior demonstrated by both participants immediately before and after the display is given; (3) the behavior accompanying the display; and (4) the components of the display.

As might be expected, these birds proved to be highly social and their various activities tended to be performed in concert. This included eating, drinking, bathing, preening, stretching, etc. Periods of such activities alternated throughout the day with periods of resting. No sexual behavior was noted during the first weeks after capture, nor in the wild birds which remained in the vicinity. The captives were subjected to normal day lengths.

Agonistic Behavior

Agonistic behavior in redpolls, as in other animals, consists in part of a number of displays which serve to reduce the attack tendency and/or to increase the escape tendency of opponents or potential opponents (see Hinde, 1956, for a discussion of the use of the term "tendency"). As in other types of displays, these agonistic displays were most pronounced when the tendencies were in greatest conflict. In the case of agonistic displays the conflicting tendencies were usually the attack and escape tendencies. Sometimes other tendencies were also present and contributed additional variables.

It is thought, as a result of the findings of many investigators working with many kinds of animals, that the attack and escape tendencies are usually, if not always, simultaneously present in any animal demonstrating agonistic behavior (Moynihan, 1955*a* and *b*). Either may be so preponderant that the animal either simply flees (escape) or attempts to supplant or fight (attack) the opponent. Commonly, however, the two tendencies are in some degree of conflict resulting in various displays depending upon the actual and relative strengths of the conflicting tendencies. In such displays, it is usually possible to recognize the presence of both tendencies by the expression of motor elements associated with the attack and the escape behavior. The relative proportion of these motor patterns may be, but are not necessarily, associated with the relative strengths of the two conflicting tendencies. Thus, between

the acts of simply fleeing and of simply attacking, there is a rather elaborate series of displays expressing varying proportions of actual and relative strengths of attack and escape tendencies. The type of display forthcoming is dependent both upon the internal state of the animal (specific action potential) and upon the nature of the external stimulus(i).

There are obviously an infinite number of actual and relative strengths of both the attack and escape tendencies between simple fleeing and simple attack. It is equally obvious that there are not an infinite number of displays which occur between these two extremes. Ordinarily only a few such displays exist, which means that each display functions within a rather broad spectrum of actual and relative strengths of tendency conflicts. This stabilization of display types within a certain amount of variability of tendency strengths has been termed "typical intensity." Morris (1957) presents a thorough discussion of this phenomenon. It might be mentioned here that the establishment of a typical intensity for a display is the result of conflicting selective pressures acting in a manner to insure maximum "understanding" of what the displayer may do next while at the same time minimizing any possible ambiguity.

It may be of value to mention here the fact that the amount of attack or escape valence cannot always be determined by the proportion of attack and escape motor elements incorporated in a given agonistic display. Once such a display has evolved and become at least partly ritualized (see Blest, in press) its threshold of response may have become shifted somewhat from its original source. Hence, a display made up of (and originally caused by) a preponderance of escape tendency may have its threshold of response shifted, through selective pressures operating until the display comes to have a high attack valence. The Spread Display of the Wood Thrush (*Hylocichla mustelina*) (Dilger, 1956) for instance, seems to have incorporated a great amount of escape motor patterns (much plumage fluffing and ruffling) but the display itself has a high attack valence. Thresholds, of course, can shift the other way and motor patterns originally associated with attack can come to have a greater escape valence. It must be remembered that any shifts in the form and/or "meaning" of displays must be coincident with the innate and/or learned "understanding" of the recipients.

Motor patterns associated with the attack tendency in redpolls consist of orientation toward another individual, locomotion toward another individual, and/or associated intention movements (see Daanje, 1950, for a discussion of intention movements). The acts of pecking, biting, holding, etc., are also, of course, associated with the attack tendency.

Motor patterns associated with the escape tendency in redpolls are orienting

away, or moving away, from other individuals as well as the intention movements for doing so.

The various plumage adjustments such as sleeking, ruffling, and fluffing, which are incorporated are all probably intention movements to locomote and/or temperature adjustment mechanisms. The discussion by Morris (1956) of these phenomena is useful in this regard. The fluffing of the plumage associated with the escape tendency (submissive display) serves an appeasement function (Front. A). This posture is similar in many ways to the posture adopted by sick, cold, or resting birds. Its use as an appeasement signal may have been facilitated by its previous association with an inactive and therefore non-aggressive state, as well as by its difference from the Head Forward Threat (Hinde, 1955–56).

Visual Displays.—The displays dependent upon conflicts caused by the presence of attack and escape tendencies are mostly variants of the Head Forward Threat posture (Front. D). This posture is characterized by the bird's crouching slightly by bending its legs at the hip, knee, and "heel"; the plumage is sleeked to varying degrees (these are all probably originally intention movements to fly); and the head is carried in line with the body and pointed toward the opponent. When the escape tendency is relatively strong the feathers of the crown are somewhat fluffed. The various fluffings associated with the escape tendency occur in situations where the escape tendency is thwarted either by an incompatible tendency such as attack (intrinsic thwarting) or by a combination of intrinsic thwarting and some external prevention of overt escape such as being confined in a cage or the near presence of a number of dominant individuals (extrinsic thwarting). If the escape tendency is not strongly thwarted the bird may merely orient away from the external source of escape stimulation or locomote away in various speeds and manners depending upon the strength of its actual or relative escape tendency. In situations characterized by strong extrinsic escape thwarting, but subjected to persistent attack by an opponent, the bird may exhibit strong fluffing of the entire plumage as well as strong "defensive threatening" (Front. B). The same sort of motor patterns may be evinced also by birds prevented from overt fleeing because of strong intrinsic thwarting (such as a strong incubation tendency, etc.) while subjected to persistent attack.

"Defensive Threat" in redpolls consists of the bird's fluffing the entire plumage, retracting the neck (both manifestations of escape) and at the same time orienting toward, and gaping at, the opponent (both manifestations of attack).

In the opposite situation (where strong attack is thwarted either intrinsically or extrinsically) there seems to be no particular associated display but merely ambivalent intention movements, expressed alternately, characteristic of the

two incompatible tendencies which have been simultaneously activated. For instance, a dominant bird with a strong tendency to feed may be approached by another individual. The dominant bird, although obviously exhibiting a very aggressive tendency and also very "hungry," often does not adopt a display but alternately demonstrates intention movements to eat and to attack.

The fact that thwarted escape is more often associated with a display than is thwarted attack probably is indicative of the fact that it is more of an advantage to an animal with thwarted escape to make its position clear to an opponent. The animal with thwarted escape is essentially indicating fear but a willingness to attack if further molested. An animal not able to flee is quite likely to avoid further attack if such information is communicated to an aggressor; hence, considerable biological advantage is gained. On the other hand, an animal with a thwarted attack usually has little if anything to lose if the actual attack has to be put off temporarily; hence, there probably is not as much selective pressure brought to bear which would tend to cause the evolution of a display in these circumstances.

Aside from the above special cases of thwarting of strong escape or attack tendencies there are several displays given by redpolls which are indicative of varying readiness to attack. Progressing from a simple orientation of the head toward the opponent (lowest indication of attack) we next find the Head Forward Threat (Front. D). This basic threat posture has been described above. Ordinarily the whole bird is oriented toward the opponent, but at low intensities only the head may be so oriented. In general, the head in any case makes the finer adjustments; the body sometimes being only roughly oriented. For instance, if the opponent is above the displaying bird, the body will remain roughly horizontal but the head will be pointed directly at the opponent. The same is true if the opponent is below the displaying bird but here the head would be lowered toward the opponent rather than raised. If it is possible for the whole bird to be oriented toward the opponent but only the head is so oriented, then the attack tendency is actually and/or relatively weak. The display with the next highest attack valence is the Head Forward with Chin-lifting (Front. E and F). Here the head is lifted in a quick perfunctory manner, sometimes several times. This action exposes the black chin and the pattern of the gonys to the opponent's view. The movement is repeated if the opponent does not, by its actions, signal some change in its mood. Other black-chinned carduelines such as the Hawfinch (*Coccothraustes coccothraustes*) and the Bullfinch (*Pyrrhula pyrrhula*) adopt a similar course of action (Hinde, 1955–56).

If the actual or relative strengths of the attack tendency continue to rise, then the Head Forward Threat is associated with Gaping (Front. G). The plumage is also more sleeked here than with the Chin-lifting, and even more so

than with simple Head Forward Threat. Gaping is quite likely to have been derived from the intention movement for biting. Sometimes Gaping and Chin-lifting occur together, but this is not as common as either is alone. Apparently the exact relative and/or actual strength limits of the attack and escape tendencies responsible for Chin-lifting plus Gaping are more restricted than they are for either of these patterns alone.

Further rise in the actual and/or relative attack tendency is characterized by various strengths of intention movements to fly at the opponent. The display here is still essentially a Head Forward Threat but the plumage is very sleeked and the wings are raised to varying extents but remain closed. The wings may merely be raised a bit from their supporting feathers, thus exposing the carpal joints or they may, in extreme cases, be raised over the back (Front. H). Raised-wing displays, particularly the higher intensity forms, are not particularly common in the redpoll, and most attacks are either effective somewhere short of Wing-raising or they become supplanting attacks in which case the Wing-raising is such a quick transitory action that it can scarcely be perceived. In extreme cases the attacker may actually peck at or bite the opponent but this is rare even in captivity where escape is difficult. I have never seen it among individuals in the wild.

Auditory Displays.—Bill Snapping, presumably another intention movement to bite, which incorporates an auditory component, was not observed in these birds although it is common in many other passerines including some other carduelines (Hinde, 1955–56).

Redpolls, however, use vocal signals in agonistic situations. The commonest is a rather harsh, sharp *cheh, cheh, cheh* sound and seems to serve an intimidatory function. It was heard usually while the birds were in the higher attack displays and was uttered by dominant individuals as a warning. A similar utterance, only higher pitched, more musical, and slower in cadence, seemed to serve as a location call among members of the flock. Interspersed among bouts of these latter vocalizations are frequent utterances of a *sweeeeeeeeee* note. This is very similar to a vocalization heard from American Goldfinches (*Spinus tristis*) and Pine Siskins (*S. pinus*). It has a rising inflection, is rather high in pitch, and is quite musical.

There were some color differences among the males, chiefly in the amount of pinkish suffusion on the breast and the presence or absence of this suffusion on the cheeks. There was no correlation between color and social position. The most dominant male (The Green ♂) was less highly colored than the least dominant male (The Red ♂). The females also exhibited some variation and one, the Green ♀, had a very faint pinkish tinge to the sides of her breast, but she was the least dominant female (sex confirmed by autopsy).

Social Hierarchy and Sexual Behavior

As an outcome of rather intense agonistic activity from the time of capture, these birds soon established a very rigid social hierarchy. This hierarchy remained with no change until certain shiftings gradually took place coincident with the slow development of sexual activities later in the season. The hierarchy was established as far as I could determine, within three days from the time the birds were placed together. The establishment of such a rigid social order implies, of course, that the facility for individual recognition is well developed.

About 600 encounters were recorded and evaluated. An encounter was recorded whenever one individual avoided another as a result of an oriented action. Actual physical contact was very rare. Hereafter, individuals are designated by their band color and sex.

The males were all dominant over the females in the non-reproductive hierarchy. Moreover, the hierarchy was a linear one running from the most dominant male, through the males to the most dominant female, and thence to the least dominant female. Very few reversals of expected outcomes of encounters were noted, and most of these were clearly "mistakes" on the part of the birds involved. In most of these cases a dominant bird would be approached rapidly and from the rear by a less dominant individual which apparently did not "recognize" the individual it was approaching (most of the individual recognition features seemed to be associated with the head). The dominant bird would flee from this "pseudo attack," evidently before it recognized the identity of the "attacker."

The order which was established, starting with the most dominant bird, was as follows: Green ♂, Yellow ♂, Blue ♂, Red ♂, Blue ♀, Yellow ♀, Red ♀, and Green ♀. A graphic representation of this hierarchy can be seen in Fig. 1A. The circles represent the individual birds. The widths of the solid bars and lines are proportional to the number of "wins" over the bird to which they are connected on the right. The shaded bars and broken lines represent "reversals" in the straight-line hierarchy. Again, the widths are proportional to the number of encounters. This method of graphically representing data was adapted from one utilized by Baerends *et al.* (1955) for demonstrating the interrelationships of sexual behavior patterns in Guppies (*Lebistes reticulatus*).

Redirected Aggression.—It can be noted that birds adjacent in the hierarchy tended to be involved in more encounters with each other than with those which were not adjacent. This is to be expected, as such birds are more nearly alike in dominance value. When it became apparent that the Red ♂ was being particularly aggressive toward females, I suspected redirection on his part. A careful note was then made of what the Red ♂ did immediately

after each losing encounter with another male, and in almost every case he immediately attacked a female, thus clearly demonstrating the redirectional nature of these attacks. Not only did he typically redirect to the females but these attacks were especially vigorous and commonly involved feather-pulling and other physical contact. For a discussion of the phenomenon of redirection see Moynihan (1955*b*). The other three males were never observed to indulge in redirectional activities of this sort but each of them, during the normal course of events, found themselves defeating other males. Not being able to defeat a male seems to be a source of rather strong thwarting in a male.

The relationship between position in the hierarchy and aggression is not clear. For instance, the Green ♂, the dominant bird, was not particularly aggressive in the sense that he most often initiated encounters which he won. On the contrary, encounters involving him were commonly initiated by other birds which violated his individual distance. If we think of this hierarchy as a straight line from the most dominant bird to the least dominant bird, it is more accurate perhaps to say that the hierarchy is due to an increasing tendency to recognize dominance rather than a decrease of aggressiveness through the same series.

There are many possible reasons why one bird should be more or less dominant than another. Possible factors tending to permit animals to be successful in agonistic encounters include such things as: physical superiority because of size, agility, good health, etc.; "psychological" superiority because of having won initial encounters; and being on some sort of territory or even in a more familiar location as opposed to the opponent. All of these could work in varying combinations to cause one individual to be more dominant than another. The reverse of the above conditions, on the other hand, tends to cause animals to be less dominant.

It must be remembered that the attack and escape tendencies have not evolved as a means to an end nearly to the extent other tendencies have, such as the sexual, feeding, and drinking tendencies, for instance. Attack and escape are almost always associated with gaining some advantage relative to other tendencies, and as such may be thought of as "service tendencies." Their expression allows an animal to gain food, water, space, mates, and escape from enemies or other undesirable or dangerous features of the environment. The use of attack and escape tendencies may, upon occasion, even be somewhat interchangeable. For instance, a bird may learn that it can approach a more dominant individual more closely if it adopts a submissive posture than it could otherwise. This might well allow this individual to feed, drink, or bathe in situations where it otherwise could not. In a case like this, the animal has profited by learned use of the escape motor patterns whereas it might

have employed motor patterns associated with aggression in the presence of a less dominant individual.

A less dominant individual near a more dominant one conducts itself in such a way as to minimize the possibility of provoking an attack. The greater the disparity between the social positions involved, the greater the care taken by the less dominant bird not to provoke an attack. Less dominant birds do not move quickly in the presence of dominant individuals. They do not approach directly and from the front, but approach indirectly and from the rear or obliquely. They avoid orienting the head toward a superior, and frequently have the plumage fluffed to some degree indicating their submissive tendency. The Green ♀, the lowest bird in the hierarchy, was almost perpetually in the Fluffed Submissive posture.

Less dominant birds in general behave as if they had a very keen awareness of the presence of superior individuals. Dominant individuals, on the other hand, essentially behave as if their inferiors existed hardly at all.

"Unprovoked" attacks were made only by the Red ♂ and then only on females to which he was redirecting. These attacks were unprovoked in the sense that the recipient did nothing to warrant them. Such attacks are provoked, however, in the sense that these females were the only available individuals to which the redirecting Red ♂ could find a safe outlet for his otherwise thwarted aggression. These females had apparently learned to leave him alone even when they became aggressive with the onset of the reproductive season.

Straight line hierarchies were also found in Red Crossbills (*Loxia curvirostra*) (Tordoff, 1954) and in the Chaffinch (*Fringilla coelebs*) (Marler, 1955). No mention of redirection being evinced by the least dominant male is made by either of these two authors. However, Tordoff does mention that the least dominant male crossbills were particularly aggressive toward females and that this "provides an outlet for aggressive drives in the males ranked low in the male peck order." Marler does not emphasize any particularly great amount of aggression of low ranking males toward females, but both of his tables on page 111 indicate that in each case the low ranking male was involved in an inordinately great number of encounters with females. This seems to be enough evidence to suggest that low-ranking male Red Crossbills and Chaffinches may also redirect to females.

Marler (1957) came to the conclusion that Chaffinches have no innate, spontaneous appetitive behavior for fighting when in non-reproductive condition. This conclusion is in accord with my findings with redpolls. Fighting (usually only displays) only occurred in response to some external situation. This was ordinarily a situation where the attacker had to violate individual distance in order to feed, perch, bathe, drink, etc. Marler expresses

his findings in this regard thusly: "When they seek fights, it can be related either to an aggressive mood aroused by external stimuli in the immediate past, or to a learned association between fighting and other activities."

After the hierarchy had been established for a few days the amount of overt aggression was markedly reduced. It was as if each bird had learned its place and the slightest reminder was all that was necessary to maintain the order. A dominant bird would merely have briefly to orient its head toward a lower ranking individual in order to cause it to retreat or stop. Often relatively very dominant birds would continue whatever activity they were engaged in at the time (husking seeds, preening, stretching, etc.) while orienting the head briefly at the opponent—with complete effect. Most of the displays occurred between individuals close in the rank order. This is to be expected as these individuals were closest in dominance and thus the attack and escape tendencies typically involved in each case tended to be closest in strengths.

Reversal of Dominance.—As the birds demonstrated gradually increasing tendencies to behave sexually, the females gradually assumed an increasing amount of aggressiveness directed toward the males. Fig. 1A shows the Red ♀, the first to demonstrate this, having increasing success against the Yellow ♂. Fig. 1B was computed from data accumulated immediately after those for Fig. 1A and shows the reversal of dominance at a further stage. It is curious to note that the females did not become dominant over the males in general but that each female tended to select a particular male upon which to bestow her attentions. The male thus singled out behaved gradually less aggressively to "his" female as well as to other females. The Red ♂, however, continued his disproportionate aggressions against females and hence was not "chosen" by any of them as the recipient of their attentions. This, in effect, made the flock one male short and both the Red ♀ and the Green ♀ concentrated on the Yellow ♂. Aggression between these two females did not increase, however.

Hinde (1955) found the same shift in dominance in several other cardueline species, for example: Canary (*Serinus canarius*), Greenfinch (*Chloris chloris*), Bullfinch, Hawfinch, and the European Goldfinch (*Carduelis carduelis*). This situation is also found in the Chaffinch (Marler, 1955). These data and those of Hinde, Marler, etc., show that males, when in non-sexual condition, are dominant over females.

The suggestion is made that if this mechanism of female avoidance of the least dominant male, because of his redirected aggression, is working in the wild then it might serve to reduce the possibility of such "weak" males from contributing to the gene pool. There is at present no evidence from the

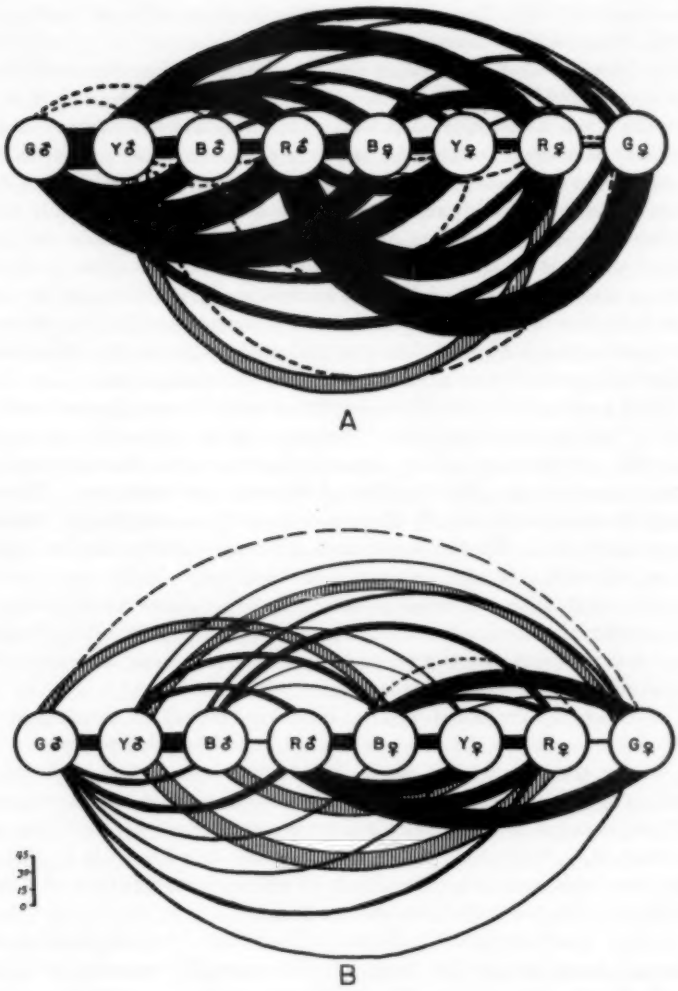

FIG. 1. Diagrams of encounters among individuals: (A) April 9 to April 22 (28 hours of observation), (B) April 23 to May 11 (38 hours of observation). Black bars and continuous lines should be read from left to right, shaded bars and dotted lines from right to left. The thickness of the bands are proportional to the number of encounters which the individual at the beginning of the bar won over the one connected to it at the end.

wild to indicate this. For a number of reasons it would seem unlikely, although the possibility remains.

The Green, Yellow and Blue males also began to sing more often and finally established territories in the small cage. Each chose a spot as far from the others as possible. The Red ♂ did not choose a territory and although he sang upon occasion, he maintained his dominance over females to the end of the investigations in early May. Actual encounters between males decreased during this early reproductive period. The songs apparently served to discourage encroachment upon the tiny territories. The males continued to feed, drink, and bathe side by side with no indication of increasing aggression among them. The fall in the amount of aggression among the males is probably due to the fact that they spent so much more time "on territory" that violations of individual distances decreased in frequency. An ordinary amount of aggression continued at feeding and watering places.

A new vocalization, other than advertising song, became apparent with the onset of this reproductive period. This was a harsh, rather high-pitched dry buzz with a speeded up ending; somewhat like the sound made by tearing a piece of coarse cloth. The function of this was not determined. This was largely because it was usually impossible to ascertain which bird uttered it at any given time. What little information I could gather seemed to indicate that it was indicative of a thwarted sexual tendency. Males were heard to give this vocalization if a female refused to be fed or if one moved away from this or other advances by the male. The advertising song, like the advertising song of many carduelines, was mainly composed of a conglomeration of the usual social and agonistic vocalizations.

The Green ♀, the lowest ranking bird, kept herself in almost perpetual fluffed posture during the non-reproductive period but changed greatly later on, during the reproductive phase, and became quite active, especially in showing aggression to the Yellow ♂. As the reproductive season progressed the females began to spend more and more time in the company of the male to which they displayed most of their aggression. The birds in the cage were now most commonly seen sitting in pairs although considerable social coherence in the entire flock was still apparent.

Another manifestation of increasing reproductive condition in these birds was the advent of "courtship feeding." This normally consisted of the male passing food to the female. The food itself was always partly digested and never whole seeds. The tendency to courtship-feed gradually increased over a period of weeks. The increase in tendency was manifested by an increase in the completeness of the motor patterns involved until finally the complete act was typically performed. This act may either be initiated by the male or by the female. The male may gently peck at the corner of the female's

mouth and she, if so inclined, will then open her mouth. The female may initiate courtship feeding by soliciting with open mouth. During courtship feeding the male stands rather erect and high on his legs, and then reaches down with his bill toward the squatting and somewhat fluffed female. Associated with the actual regurgitation of food by the male is a small amplitude, laterally-rolling vibration of the head which lasts for about a half second for each regurgitation. If the female, amenable to being fed, does not proffer her bill promptly when the male is ready with a beakful, he rapidly vibrates his mandible and tongue up and down with the bill slightly opened. This usually suffices to induce the female to permit a feeding contact. If it does not suffice, the male will then gently peck at the corner of the female's mouth. Feeding contacts ordinarily last for several seconds and sometimes as long as a minute or two. The food is rapidly pushed into the female's mouth with quick piston-like motions of the male's tongue. A bout of bill wiping by both individuals immediately follows the feeding bout. Sometimes the bills become rather generously daubed with the pasty white food.

Indications of courtship feeding began in early April. At first these were little more than repetitive gentle pecking by the males at the sides of the bills of the females. The postures of the two birds were always as described above even though the tendency to perform the feeding act was typically very low. A little later the motor patterns of the actual food regurgitation and transfer appeared but no food was actually passed. The complete act was ordinarily performed by a little past the middle of April. The frequency of occurrence of "normal" courtship feeding increased until the end of April. At this time the tendency for the males to perform this act waned markedly. The females, however, retained a strong tendency for being fed. After the first week in May courtship feeding remained a common activity but usually involved two females. It seems likely that this condition was an artifact of the conditions of captivity. It may be that because the birds were not able to perform the normal reproductive cycle, including the holding of adequate territories with the associated privacy of the pairs, the males were caused to cease their courtship feeding activities abnormally early, thus causing the females to resolve their still strong courtship feeding tendencies among themselves.

This "pseudomale" behavior on the part of the females which fed other females might be expected to be performed by females relatively higher in the dominance order than those being fed (see the excellent review paper by Morris (1955) on this subject). This was typically not the case. All of the females participated in this behavior but in the vast majority of cases the Yellow ♀ was the recipient and the Red ♀ the one assuming the "pseudomale" behavior. There were but four cases observed involving a dominant

female feeding a less dominant one, (Blue ♀ feeding Yellow ♀). The Red ♀ was observed to feed the Yellow ♀ 35 times. The reason for this is not clear to me. It may be tied up with the fact that females are normally dominant to males during the sexual phase of their behavior and/or it may be because the Yellow ♀ had an abnormally low threshold for being fed. Even when the males were feeding the females, the Yellow ♀ was the commonest recipient of food. Even though the Yellow ♀ was the usual partner it was the Blue ♂ with which she finally paired, but he was never seen to feed her! The Blue ♂ did not feed any female very much although he sang more persistently than did any of the other males. The Red ♀ was seen to be fed by males only twice; once by the Green ♂ and once by the Blue ♂. A very fleeting feeding contact was once observed in which the Red ♀ fed the Yellow ♂ (the only case of a female feeding a male observed). The Yellow ♂ was once seen briefly to feed the Red ♂ (the only male-male feeding observed). In this latter case the male demonstrating the "pseudofemale" behavior was the less dominant individual.

Unfortunately, I was forced to terminate my observations on these birds early in May and was unable to follow this behavior any further. Cursory observations past early May were enough to reveal the fact that the females finally became totally dominant over their males and that Red ♂ never gave up his redirected attacks.

The following spring at Cornell University I liberated two pairs of these birds into a large (16 feet by 22 feet by 8 feet high) outside flight cage adjacent to my office. The remainder of the original birds had been liberated with the exception of a few kept in cages in the laboratory. The flight cage was densely planted in places with *Viburnum* bushes or small hemlocks. Nevertheless, the birds never successfully nested, although further sexual behavior was observed. This included further male sexual displays, copulations, and low intensity nest building.

The male displays mentioned above consisted of a posture oriented at the female and looking very much like a Wings-raised Horizontal Threat, except that the wings (held out horizontally from the body) were spread and quivered. This would be shown for many seconds at a time. The head was often tipped up slightly and the mouth held open. Males in this posture would make tiny, quick hops along a perch or on the ground toward the female. No associated vocalizations were noted although they may have been very faint. The males also performed another display which seemed to be derived from inhibited mounting of the female. This consisted of a "moth-flight" (rapid wing beats of small amplitude) while hovering just above a perched female. If the female responded by crouching, slightly spreading and quivering her wings, and raising her head and tail, the male would immediately land

on her back and attempt copulation. The duration of copulations were usually about three seconds. The female would immediately afterward ruffle and shake her plumage and engage in a bout of preening. The male usually flew off some distance and began advertising song from one of his song perches. Males also occasionally were seen to preen after copulations.

The low intensity nest building observed consisted of females gathering fine pieces of grass, rootlets, etc., and carrying one or more bits of the material about the aviary for some time. Her male would ordinarily follow her about while she was so engaged and, more frequently, would engage in both the Head Forward Threat type display or the "moth flight" display.

Experiments on the Effects of Starvation and Proximity

Shortly after the 31 redpolls were captured, experiments were conducted to investigate the effects of starvation and proximity on agonistic behavior. All birds were in the non-reproductive condition during the course of these studies.

Since food and water were continually available, hunger and/or thirst had little or no effect on the social order. Most of the encounters, as mentioned above were caused by violations of individual distances. The only effect of hunger shown by birds that were equally deprived of food for a short period (three or four hours) and then presented with food, was to prompt less dominant birds to be more "reckless" about violating the individual distances of more dominant birds. This, of course, increased the number of encounters but their outcomes did not even temporarily upset the established hierarchy. The effects of differential starving on dominance have not as yet been studied. The starvation experiments were repeated a number of times and longer periods of starvation prompted greater numbers of encounters than did shorter ones.

I have noticed that during the winter ordinarily inferior Tree Sparrows (*Spizella arborea*) in possession of a food source became temporarily higher in dominance until their tendency to eat had markedly waned. These birds dug little pits in the snow in order to expose seeds which had been placed out for them. Such birds would often dig themselves nearly out of sight. Less dominant birds would vigorously defend their pits against ordinarily more dominant birds and would be successful until they had eaten for some time; after which they could be driven off by these dominant individuals. The relationships among hunger, thirst, aggression, and dominance are not at all clear as the evidence so far is somewhat conflicting. Marler (1955) studied the effects of starvation on the social order of Chaffinches and had results similar to mine for redpolls, and the same may be said in regard to Andrew's (1957) study on *Emberiza*.

In order to study the relationship between proximity and aggression in redpolls I constructed two identical food hoppers which were placed side by side and fashioned in a manner which allowed them to be slid along a horizontal rod calibrated in centimeters. The feeding apertures of the hopper could thus be placed at various distances from one another. This set-up was essentially similar to one used by Marler (1955) in order to investigate the same phenomena in Chaffinches. His results were similar to mine. Unfortunately, I was obliged to discontinue the investigations before an adequate amount of quantitative data became available. The females tolerated each other at much closer distances than did the males. The distances involved were about 4 cm. between females and about 10 cm. between males. Heterosexual combinations were intermediate at about 7 cm. The equivalent distances for Chaffinches (Marler, 1955) were 7 to 12 cm. for females, 18 to 25 cm. for males, and 8 to 12 cm. for heterosexual combinations. Marler found that there were some differences among various flocks in this regard. Some individuals were also more tolerant than others regardless of their positions in the hierarchy. Thus the most dominant male was not necessarily the least tolerant individual. These findings were also in agreement with my observations on redpolls except I had no measure of flock differences since I worked mostly with but one flock.

The distance measurements stated are indicative of a zone, rather than an abrupt threshold distance. This zone is measured as the distance at which approximately half of the time individuals would be tolerated and half of the time not tolerated. Birds showing some indication of submissive behavior (plumage fluffing) were tolerated at closer distances than those demonstrating some intensity of aggression. Again these findings agree with those of Marler (1955).

The initial vigor demonstrated by the various birds of the flock in their agonistic encounters may have played a role in the eventual determination of the social hierarchy. All birds were placed together at the same time so that prior residence did not have a bearing on social position. It may have been that at least some of these birds "knew" each other in the wild and this may have had a bearing on the eventual social structure in the cage.

I am indebted to the R. T. French Company of Rochester, New York, for financial aid enabling me to pursue this study, and also to Dr. Edward Warner of St. Lawrence University for his friendly cooperation and for making the facilities of the Department of Biology available.

Summary

Thirty-one captive redpolls were studied in the laboratory but only eight of them (four males and four females) were studied intensively. Their agonistic behavior was described and evaluated, and the Head Forward

Threat display and its variants were found to be the chief displays indicative of varying readiness to attack. They have the usual passerine fluffed submissive posture and employ a defensive-threat display involving simultaneous submissive patterns and attack patterns.

This flock of eight birds quickly developed a linear hierarchy beginning with the most dominant male and running to the least dominant female. This is similar to hierarchies found in captive Red Crossbills and Chaffinches. The least dominant male showed an unusual amount of aggression to females and this was demonstrated to be caused by redirection.

Each female eventually, as the birds gradually began to behave sexually, became dominant over a particular male. This reversal of sexual dominance is known for several other species. The least dominant male was never "chosen" by a female, presumably because of his continuing history of redirected aggression.

Mild starvation of a few hours increased the number of encounters but did not affect the social hierarchy. It was found that females tolerate each other at smaller distances than males tolerate each other. Heterosexual combinations were intermediate in this regard.

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LABORATORY OF ORNITHOLOGY, CORNELL UNIVERSITY, ITHACA, NEW YORK, APRIL 9, 1959

NEW LIFE MEMBER

Mrs. G. Hampton (Elizabeth Taylor) McGaw, a graduate of Mount Holyoke College (B.A.), has been interested in birds for many years, strictly as an amateur. Forty years ago Mrs. McGaw taught bird and other nature study to her Camp Fire Girls, then began speaking before women's clubs and granges on the economic value of birds, and now is an active and generous supporter of conservation organizations. She is a life member of the American Forestry Association, the New Hampshire Audubon Society, and is becoming a life member of the A. O. U.

A QUANTITATIVE STUDY OF SEXUAL BEHAVIOR OF MALLARDS AND BLACK DUCKS

BY PAUL A. JOHNSGARD

In recent years an increased interest in the use of behavioral characteristics in evolutionary studies has developed, and this is particularly true in the case of waterfowl. The classical studies of Heinroth (1911), who was one of the first to apply knowledge of waterfowl behavior to systematics, have been elaborated on by Lorenz (1941; 1951–1953) in his important contribution toward the understanding of relationships in the Anatinae. These, and other, studies have stressed the qualitative behavioral differences occurring among different species as providing possible isolating mechanisms through their presumed function of conveying species-specific recognition signals. To the present, no extensive quantitative studies of the behavior of very closely related forms of waterfowl have been undertaken, although Dr. D. F. McKinney's still uncompleted studies on the races of the Common Eider (*Somateria mollissima*) will provide an important contribution in this field. By studying the reproductive behavior of such closely related forms the evolution of isolating mechanisms can be fruitfully studied in their early stages and thus provide an insight into the general process of speciation.

As part of a more general study (Johnsgard, 1959) concerning the evolutionary relationships between the Mallard (*Anas platyrhynchos*), the Black Duck (*Anas rubripes*), and other closely related forms, behavorial characteristics were utilized as taxonomic characters. The results of this general study, which will be published later, indicate that the Black Duck is much more closely related to the Mallard than is generally supposed and that the two forms should probably be considered to be only subspecifically distinct. The purpose of the present paper is to summarize the quantitative aspects of the behavioral studies and to discuss their probable significance in terms of (1) the evolution of behavioral isolating mechanisms; (2) the relative importance of display and plumage in species-recognition signals of these birds; and (3) the concepts of response specificity and response thresholds, or "drive."

Methods and Objectives

Observations were made over a two-year period on flocks of Mallards and Black Ducks in the Cayuga Lake region of New York. Mallard observations were carried out in large part at Stewart Park, Ithaca, where a semi-tame flock of approximately 200 birds is present the year around. Wild Black Ducks were observed primarily at the Howland's Island Game Management Area, near Port Byron, New York, where large numbers (1000 to 2000) of

these birds winter with the waterfowl breeding stock of the New York State Department of Conservation. Wild Mallards also winter at Howland's Island, and supplementary observations on this form were made there. Most observations were made with the aid of a 20-power spotting scope, and approximately 1000 feet of 16 mm. motion picture film were exposed and analyzed for critical comparisons between the two forms.

For the use of camera and projection equipment I extend my sincere thanks to Dr. W. C. Dilger. I especially express my deepest appreciation to my graduate committee chairman, Dr. C. G. Sibley. Dr. L. C. Cole suggested certain statistical analyses. The study was financed in part by fellowships from the Cornell University Graduate School and the National Science Foundation.

Although the sexual displays of the Mallard are well known (e.g., Lorenz, 1951–1953; Weidmann, 1956; Ramsay, 1956), very few observations on the corresponding displays of the Black Duck have been published. The few which have been published, such as those of Trautman (1947) and Wright (1954), have dealt for the most part with copulatory behavior or aerial chases. According to Ramsay (1956) and Delacour (1956), Black Ducks differ in their sexual behavior from the Mallard only in that the "Head-up-tail-up" and "Nod-swimming" displays are independent in the former, but are linked in the latter. (Names given displays are those of Lorenz, 1951–1953, and detailed descriptions of them can be found in that paper or in those by Ramsay, 1956, or Delacour, 1956.) Cursory observations of Mallard and Black Duck displays soon made it clearly apparent that courtship patterns of the two forms are extremely similar, and motion picture analysis failed to establish any qualitative differences between them. However, it was believed that possible differences might be present which could take the form of (1) differences in frequencies of the various male displays, (2) differences in seasonal periodicity of displays, or (3) differences in the contextual occurrence of the various displays in the two forms.

With this in mind, it was decided to record the male responses which were usually elicited by unmated females and which could conceivably act as potential isolating mechanisms by providing specific recognition signals. There are three such responses, those called by Lorenz (1951) the "Grunt-whistle," the "Head-up-tail-up" with associated "Nod-swimming," and the "Down-up." Other male responses, such as "Mock Preening" and copulatory behavior, either occur very rarely or are of uniform nature throughout a wide range of species and thus probably could not function effectively in species recognition. The total number of each of the three mentioned male displays observed during each "bout" of display was tallied. A "bout" could range from a single male display to five or more males displaying simultaneously

with the same or different movements toward a single female. The accurate recording of such combined displays involving several drakes has an obvious limit, depending upon the experience of the observer and the limitations of human perceptive powers. This limit, in my case, is approximately five birds. Fortunately, displays involving more than five birds displaying simultaneously were relatively rare. For the present purposes, "simultaneous" means that no noticeable temporal break occurred between the end of the first male display and the beginning of the last display. Each display in a bout involves a different male, since no male was ever observed to perform two displays during a single bout (the Head-up-tail-up and Nod-swimming are considered as a single display unit). A total of over 3000 Mallard and over 1300 Black Duck displays were recorded in this manner from September, 1958 through April, 1959, and form the primary basis for the following results and discussion.

Results

Seasonal Periodicity.—No definite differences in seasonal periodicity of displays were found. Mallards were observed displaying sexually as early as September 13, and Black Duck sexual displays were observed on the first trip to Howland's Island on October 11. The frequency of Black Duck displays observed at that time, however, indicated that they had begun considerably earlier. In Table 1 is presented the frequency of displays observed for Mallards and Black Ducks on a unit-time basis for the period September through April, and some idea of seasonal periodicity can be derived from these data. However, total numbers of birds under observation varied considerably, both between the two forms and at different times for a single form, and this makes close comparisons impossible. In addition, cold temperatures, wind, and disturbance had strong depressing effects on display frequency during any time period, and these factors also complicate the picture. Disturbance was a particularly important factor in the case of Black Ducks, which were a hunted population, and this single factor accounts in large part for the considerably lower overall frequency of courtship activity observed in that form.

Taking all of these factors into account, it was apparent that the largest numbers of birds were displaying sexually during November and December (Fig. 1). Sexual displays tapered off during the cold weather of January, and increased again in February and March. Displays were seen, sporadically, until the end of June, although females began laying early in April. However, the great majority of displays being observed from February onward was accounted for by the relatively small percentage of males not already mated, and the actual major period of sexual display appears to occur in

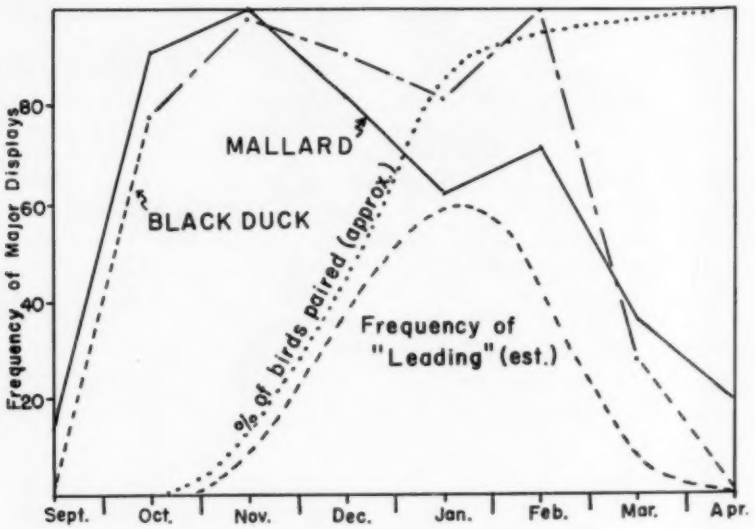

FIG. 1. Relation of approximate period of pair formation in Mallards and Black Ducks to relative frequencies of major male displays and "Leading" display.

November and December in both the Mallard and the Black Duck. These figures agree fairly well with those presented by Ramsay (1956), who found (in Maryland) a peak display frequency in December and January. The period of time required for individual pair formation in both Mallards and Black Ducks is probably much longer than is generally appreciated, and although some evidence of pairing was observed as early as late October, such pairs often appeared to be temporary. The period of pair formation does not seem clearly correlated with either the frequency of copulation (which was highest in October and November) or with the gonad cycle (Höhn, 1947), since the testes do not begin to recrudesce until the lengthening photoperiod provides a mechanism for gonadal stimulation. Stotts (1958) found a gradual increase in the percentage of paired Black Ducks from about 10 per cent in late September to about 60 per cent by April, and then rising sharply to nearly 90 per cent by early May. My own estimates of the period of major pair formation are indicated in Fig. 1, and are rather earlier than Stotts' estimates. I agree with Höhn (1947), who believed that the primary function of sexual display is in the formation of pairs, and that fall and winter copulations may serve to strengthen the bond between incipient pairs. It cannot be doubted, however, that a great many copulations occur between non-mated

birds, and that therefore copulation *per se* appears to be relatively unimportant in pair formation. The apparent means by which pair formation is effected in Mallards has been discussed by Weidmann (1956), and my observations bear out his conclusions. In short, it may be stated that female Mallards (and Black Ducks) actively "select" potential mates by "Inciting" (Lorenz, 1951) them against other birds. The male response to such Inciting may be to attack the indicated individual (usually another male) or, more often in preliminary stages of pair formation at least, to respond with a special display I have termed "Leading" (Johnsgard, 1959). This display involves an orientation of the back of the male's head toward the Inciting female while swimming rapidly ahead of her. Which factors of display and/or plumage result in the selection of a specific drake by a female are still uncertain, but a few observations on this point will be discussed later.

Individual Display Responses.—In Lorenz's studies of the Mallard (1951), he concluded that the three major male displays were "of equal value," and whichever one was performed by a male was largely a "matter of chance." However, Lorenz's student Weidmann (1956) investigated this point and concluded that this is not the case. Weidmann's opinion was that the Grunt-whistle display indicates a low intensity courtship whereas the Down-up and the Head-up-tail-up displays are indicative of high intensity courtship situations. Thus, of a total of 1074 individual male displays of these types he recorded, he found that the Grunt-whistle was usually performed when a single male displayed toward a female. During displays where many males reacted simultaneously, the Head-up-tail-up or Down-up displays were usually performed. As shown in Table 1, my observations support Weidmann's conclusion that the displays are not of random occurrence or of equal probability of elicitation, since there are distinct differences in frequency of the three displays during the same time period, and of individual displays during the course of the entire pair formation period. In both the Mallard and the Black Duck the Grunt-whistle tended to be the most frequent display during the first few months of pair formation, and the Down-up tended to be least frequent. As time progressed, however, the Down-up became more frequent and comprised about half of the total male displays during peak pairing activity. This increase of Down-up displays was achieved primarily by the reduction in frequency of the Grunt-whistle in the Black Duck and the Head-up-tail-up in the Mallard. These figures thus corroborate Weidmann's opinion that the display performed most frequently during low intensity courtship situations early (and very late) in the season is the Grunt-whistle. However, in the present case the data also point to the conclusion that the Head-up-tail-up and Down-up are not equivalent either, but that the Down-up represents

TABLE 1

SEASONAL FREQUENCIES OF MAJOR MALE DISPLAYS

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Total
Grunt-whistle									
Mallard	40(42%)	279(45%)	379(46%)	170(38%)	59(35%)	150(35%)	102(42%)	74(41%)	1250
Black Duck	—	66(41%)	148(30%)	34(26%)	62(27%)	43(15%)	5(19%)	—	358
Head-up-tail-up									
Mallard	35(37%)	185(29%)	202(25%)	95(21%)	19(11%)	71(16%)	41(17%)	46(26%)	694
Black Duck	—	64(40%)	200(41%)	36(28%)	81(35%)	108(38%)	8(31%)	—	497
Down-up									
Mallard	20(21%)	163(26%)	239(29%)	187(41%)	90(54%)	212(49%)	101(41%)	49(33%)	1071
Black Duck	—	30(19%)	144(29%)	60(46%)	86(37%)	133(47%)	13(50%)	—	468
Total Displays									
Mallard	95	627	820	452	168	436	244	179	3018
Black Duck	—	160	492	130	229	284	26	—	1321
Total Bouts									
Mallard	52	464	467	303	104	234	151	122	1897
Black Duck	—	76	237	74	132	144	10	—	673
Displays/Bout									
Mallard	1.8	1.3	1.8	1.5	1.6	1.9	1.6	1.4	1.6
Black Duck	—	2.1	2.1	1.8	1.7	2.0	2.6	—	2.0
Frequency of Display*									
Mallard	.13	.91	1.0	.82	.61	.71	.35	.20	—
Black Duck	—	.78	.98	.91	.81	1.0	.27	—	—

*Per unit of time, relative to month having highest frequency.

the highest intensity display since it occurs most frequently during the period of very intensive display.

It is of interest that the Head-up-tail-up, the most spectacular and complicated of the three displays, is apparently a lower intensity reaction than is the Down-up, which is a relatively simple display. However, it may be significant that, of the three displays, the Down-up has the narrowest range of interspecific occurrence, being restricted as such to the Mallard group and, in rather modified form, to the Gadwall (*Anas strepera*) (Lorenz, 1951–1953). The Grunt-whistle is of much wider distribution, occurring in the Mallard group, the Gadwall, the Green-winged Teal group (*Anas crecca, A. flavirostris*, etc.), the Pintail group (*Anas acuta, A. georgica*, etc.), and others. The Head-up-tail-up display also occurs in most of the species which possess the Grunt-whistle display. Thus the Down-up may be the most important of the three displays from the standpoint of recognition in Mallards, even though it is not the most complex.

To test the hypothesis that the three displays represent a hierarchy of reaction intensities, it must be hypothesized that the lowest intensity display would, since it results from low intensity stimulation, tend to occur most frequently as isolated displays. Conversely, when the female's behavior provides a strong stimulus, it would be expected that larger numbers of males would tend to respond simultaneously with one of the higher intensity displays. By determining the frequency with which a given display is performed by a single male, two males, etc., to the maximum number of males observed to perform a display simultaneously (i.e., during a single bout), this hypothesis can be tested. In Figs. 2 and 3 are presented such data for Mallards and Black Ducks. It will be noted that in both forms the Grunt-whistle occurs more frequently as a single display than does either the Head-up-tail-up or the Down-up. This latter display is more frequently performed simultaneously by several drakes than is either of the other two. These data thus correlate well with the supposition that the Grunt-whistle is the lowest intensity reaction and the Down-up represents the highest intensity reaction, with the Head-up-tail-up being intermediate.

At this point the assumption is that multiple simultaneous displays of a single kind are the result of a specific stimulus from a female and not simply the result of a contagious or mimetic effect resulting from several males "imitating" the display performed by the first male to respond. Although this possibility is almost impossible to test experimentally, it can nevertheless be tested statistically. That is, if the males are reacting completely independently of one another the frequency distribution patterns shown in Figs. 2 and 3 should follow a Poisson distribution, whereas if any contagious effect is present such a distribution will not obtain. A typical Poisson dis-

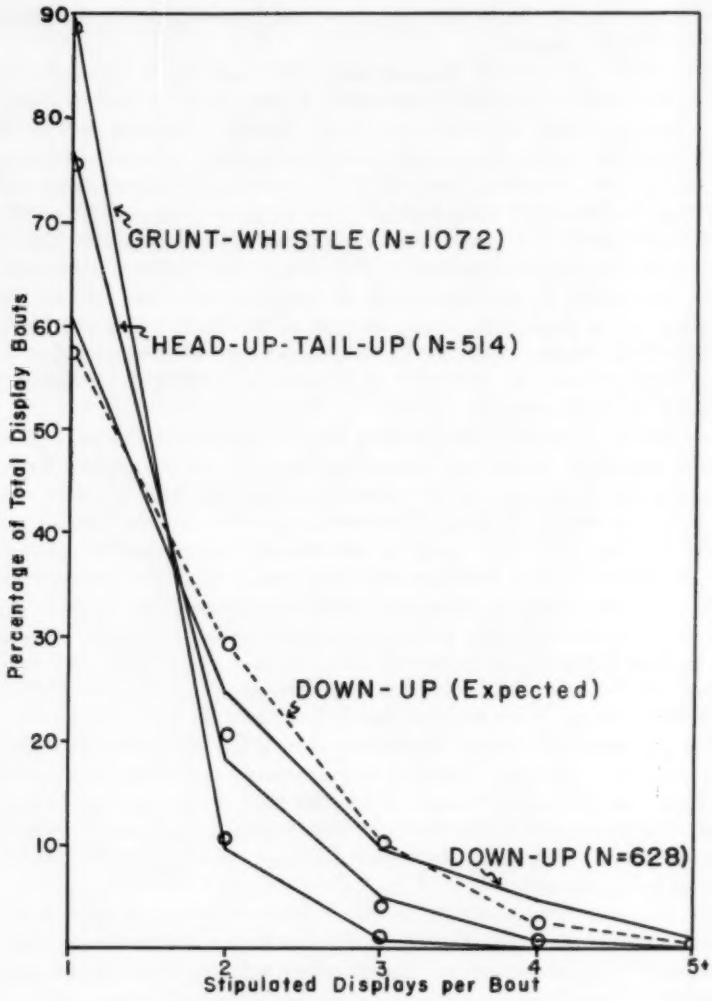

FIG. 2. Frequency distribution patterns of displays per bout observed in male Mallards. Solid lines connect observed frequencies; open circles (connected by dotted line in the case of Down-up) indicate calculated frequencies based in Poisson distributions. "N" equals number of bouts involving each of the indicated displays.

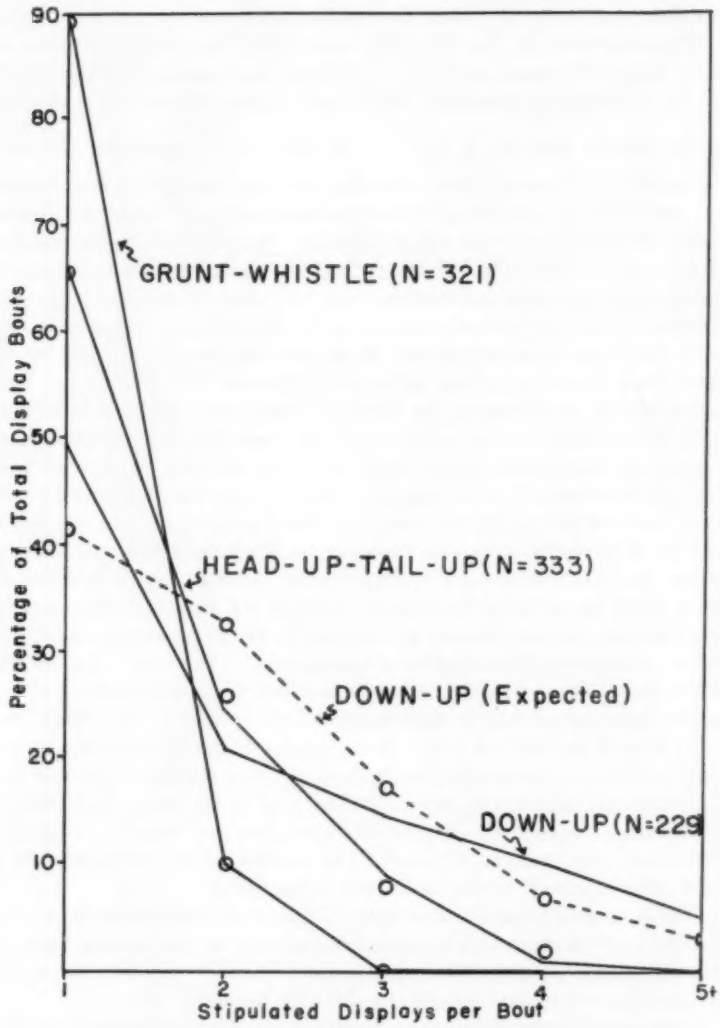

FIG. 3. Frequency distribution patterns of displays per bout observed in male Black Ducks. See Fig. 2 for explanation of symbols.

tribution contains a "O" frequency category, which in the present instance is unmeasurable since one obviously cannot tally the number of times no males displayed toward a female. However, this unmeasureable category can be accounted for (van Rest, 1937), and a mean Poisson value obtained by the general formula: $\bar{X} = \frac{m}{1 - e^{-m}}$. In this case $\bar{X}$ equals the observed, and m the actual, mean. After obtaining this value, the distribution in question can be tested to determine if it can be described by a Poisson distribution having the same mean as the calculated mean. This tended to be the case (see Figs. 2 and 3), for in both the Mallard and the Black Duck the Grunt-whistle and the Head-up-tail-up distributions could be explained ($p=.05$) by Poisson distributions having various means. For the Mallard these means were 0.23 and 0.54 for the Grunt-whistle and Head-up-tail-up, respectively, and for the Black Duck the corresponding values were 0.23 and 0.79 displays per bout. In the case of the Down-up, the observed distributions deviated sufficiently from the calculated ones to be rejected at the 5 per cent level, mainly because of too many observations in the categories of four displays or more per bout. The calculated mean Poisson figures for the Down-up were 1.03 and 1.59 displays per bout for the Mallard and Black Duck respectively. In the case of both the Head-up-tail-up and the Down-up, the Black Duck had a significantly higher ($p=.01$) number of displays per bout. Thus it may be said that the Black Duck has a lower threshold to perform the Head-up-tail-up and the Down-up than has the Mallard, as indicated by the larger average number of males performing these displays simultaneously. This may also be concluded from Table 1, in which it may be seen that the average number of total males displaying per bout is significantly higher ($p=.01$) in the Black Duck (2.0) than in the Mallard (1.6). If the relative frequency of total male displays per bout is plotted graphically (Fig. 4), this difference becomes even more apparent, and it will at once be seen that in the Black Duck multiple simultaneous displays are considerably more frequent than in the Mallard (difference significant at .01 level). The possible biological significance of these differences will be discussed later in the paper.

Finally, it may be said on the basis of the fit obtained using the Poisson distribution that males tend to react independently of one another when displaying (except possibly in the case of the Down-up), and thus presumably are reacting to a mutual specific stimulus (the female).

Combined Display Responses.—Simultaneous displays involving two or more males are frequently "mixed," rather than "pure," and may at times involve all three of the male display patterns. This is indicated in Figs. 5 and 6, in which the percentage composition of the three displays is indicated for all display bouts recorded involving from one to five or more males.

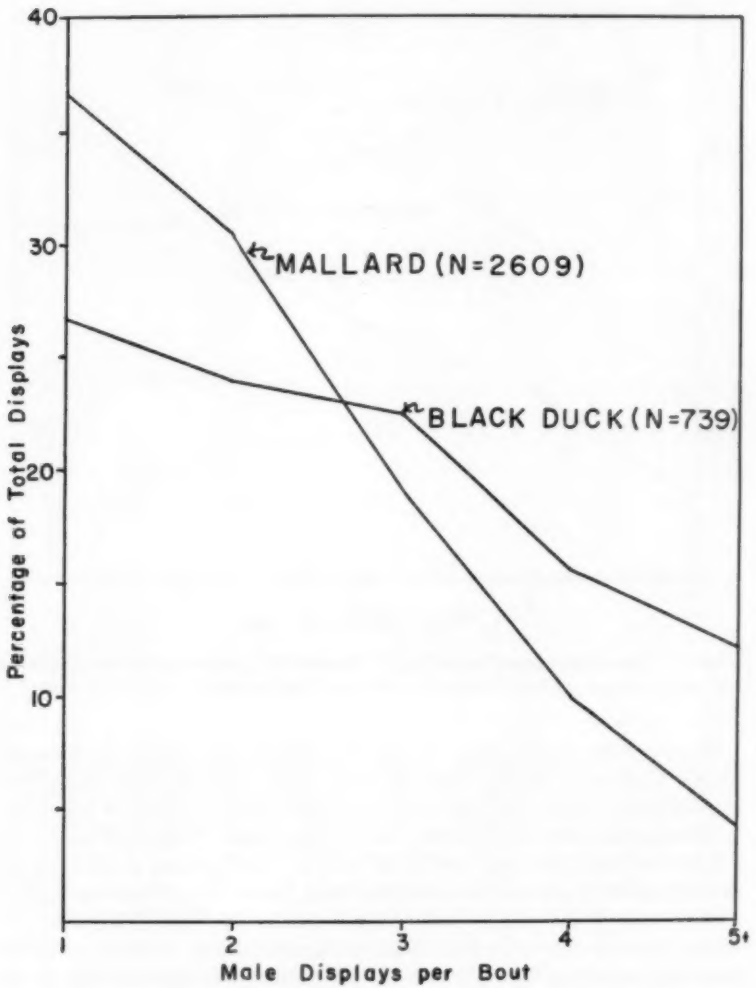

FIG. 4. Total male displays per bout observed for male Mallards and Black Ducks. "N" equals total number of displays included in sample.

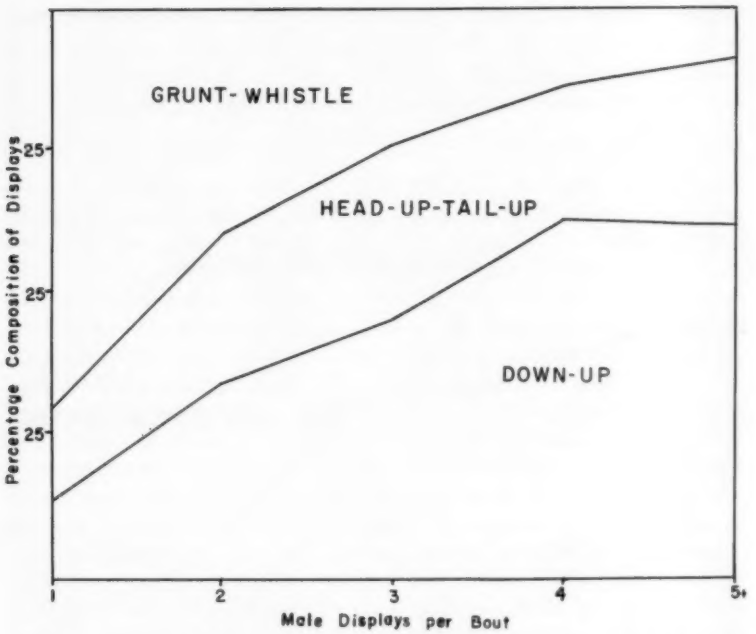

FIG. 5. Percentage composition of major Mallard displays relative to the number of total male displays per bout. Based on 2609 total male displays.

These graphs clearly point out the fact that Grunt-whistles predominate when a single male displays, that Down-ups predominate in bouts where four or more males display, and that Head-up-tail-ups tend to occur most frequently in intermediate situations involving two or three birds. Thus, of all the Grunt-whistles recorded, 58.0 per cent of the total occurred as lone displays in the Mallard and 45.6 per cent as such in the Black Duck. Of all Head-up-tail-ups, 60.3 per cent in the Mallard and 65.2 per cent in the Black Duck were performed when two or three birds displayed simultaneously. Finally, of all the Down-ups recorded, 26.4 per cent in the Mallard and 56.8 per cent in the Black Duck occurred when four or more birds displayed simultaneously. This relatively low per cent of Down-ups in the case of the Mallard suggests that Mallard males are less specific in their response to strong stimulation than are Black Duck males. More will be said of this later.

Field observations indicated that these three displays actually tend to represent graded responses to three increasing strengths of female stimuli.

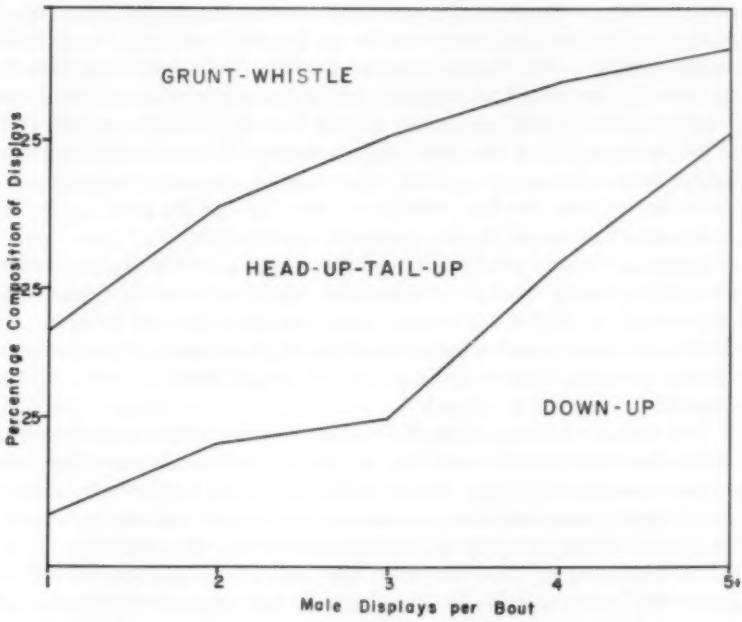

FIG. 6. Percentage composition of major Black Duck displays relative to the number of total male displays per bout. Based on 739 total male displays.

Thus, an Inciting female corresponds roughly in stimulus valence to a male Grunt-whistle response, Nod-swimming parallel to or away from a male corresponds approximately to the Head-up-tail-up response, and Nod-swimming toward a male (the strongest female stimulus) almost always results in the Down-up response. However, an unvarying one-to-one stimulus-response (or "sign stimulus"-"fixed action pattern" in ethological terms) cannot be supported by these data, since the percentage of Down-up displays varied greatly as the season progressed, but the number of male displays per bout remained relatively constant (see Table 1). Thus, a female stimulus which is sufficient to elicit a Down-up response later in the season would, in September or October, for example, most likely result in a Grunt-whistle or Head-up-tail-up. Nod-swimming by females tends to decrease later in the season (Ramsay, 1956), although it was observed as late as April in both forms. Inciting is much more common during this later period, and the male responses tend to shift

from the three major swim displays to the Leading display described earlier, with several males often competing for the Leading position in front of the Inciting female. This Leading display may thus be thought of as possibly representing the highest intensity male response, and it seems very likely that it may have the greatest importance in mate selection of all the male displays. With the beginning of the male Leading displays in late October, courting groups became much more mobile and animated, and male competition became very evident. In their attempts to attain the Leading position, trailing males often made short flights (probably equivalent to the "Jump Flights" of Lebret, 1957) and landed a short distance in front of the Inciting female. Leading was most evident during December and January (when it was usually observed 20 to 30 times per hour) and tapered off in late February and March, and thus was most frequent during the period of apparent formation of pairs. It was, however, observed until the end of April in greatly reduced intensity.

This variable intensity of male displays, associated with constant or even decreasing female stimuli, seems explainable by hypothesizing a varying male response threshold to sexual stimuli. This may be the result of sex hormone level changes associated with testis growth, but no data on seasonal changes in Mallard androgen levels are available for testing this possibility. However, merely saying that the males have an increased sexual "drive" or "tendency" seems to avoid the basic question and does not contribute to its solution.

A crude measurement of this seasonal change in male response thresholds can be obtained by comparing the monthly percentage frequencies of the Down-up display, the highest intensity response of the three displays. These data suggest that the lowest male Mallard display thresholds occur in January and February. Data for the Black Duck, which are much less reliable, indicate low thresholds from December through March. Therefore, this period of low response thresholds does not fit well with the gonad cycle, since the testes do not begin to recrudesce until day-length begins to increase, and males remain sterile until mid-February (Höhn, 1947). In addition, display intensity tapers off in April, although gonad size is at a maximum during this time. Presumably, male hormone levels are closely related to gonad volume or size, which varies immensely in these birds, and this casts doubt on a close connection between male response thresholds and male hormone levels.

Specificity of Response.—Weidmann (1956) believed that simultaneous group displays involving Down-ups and Head-up-tail-ups tended to show a higher frequency of "pure" displays than one would expect to result from chance which, since mimesis is apparently not important, implies that the males tend to respond specifically to female stimuli. Weidmann's conclusions

appeared, judging from his tabular data, to be based on 78 bouts of display. This conclusion seemed important enough to warrant further investigation, so the frequencies of all recorded combinations of these two displays have been determined for the Mallard (927 bouts) and Black Duck (456 bouts), and are presented in Tables 2 and 3. Inclusion of Grunt-whistles, which would have necessitated the construction of a three dimensional table, did not seem justified because they form a very minor component of multiple displays (see Figs. 2 and 3).

As a measure of the randomness of response, the expected frequencies of each of the possible combinations of these two displays can be calculated for each sample of bouts involving a given total number of males perfoming the two displays. That is, if the male responses are random in nature, they should "segregate" according to the random probability frequencies for each combination class. Such expected frequencies have been calculated, and are placed in parentheses below the observed frequencies of each combination class. An index to the relative "purity" of male response is obtained by comparing the number of observed "mixed" display bouts to the expected number. Thus in the Mallard 141 bouts of "mixed" displays were observed, whereas 224 would have been expected on the basis of random response (62.9 per cent of the expected). In the Black Duck 90 out of a calculated 158 expected bouts were recorded, or 57.0 per cent of the expected. In both cases the differences are highly significant (p less than .01), and it may be concluded that male Mallards and Black Ducks do tend to respond specifically to female stimuli. That such a response specificity exists should not be surprising, and the above technique seems to provide a useful measure of the degree of response specificity.

Individual Variation in Response.—Sources of individual variation are presumably of two types, namely variations in intensity of performance of the various displays by a single individual as a result of variations in its internal state or the strength of the external stimulus and, secondly, genetic variation among different individuals in the population. Since only unmarked birds were studied it was not possible to completely separate these two variables, but some pertinent observations might be mentioned here.

According to Delacour (1956) and Ramsay (1956), Mallards differ from Black Ducks in that the Head-up-tail-up display is linked to the subsequent Nod-swimming in the Mallard, whereas in the Black Duck the two displays are independent. Of 665 Mallard Head-up-tail-up displays I recorded, 625 (94.3 per cent) were followed by Nod-swimming, whereas in the Black Duck 479 out of 490 (97.7 per cent) were followed by Nod-swimming. Thus the two displays are actually strongly linked in both forms, and the statements of Delacour and Ramsay to the opposite effect are not supported by my

TABLE 2

RECORDED BOUTS OF MALLARD DISPLAY COMBINATIONS

		Males Performing Head-up-tail-up Display					
		0	1	2	3	4	5
Males Performing Down-up Display	0		258 (258)	65 (60)	17 (15)	1 (2)	1 (0)
	1	258 (258)	70 (120)	16 (30)	4 (9)	2 (2)	
	2	104 (60)	30 (30)	5 (14)	2 (4)		
	3	57 (15)	8 (9)	2 (4)			
	4	20 (2)	2 (2)				
	5	5 (0)					

data. In the small percentage of cases where Nod-swimming did not follow the Head-up-tail-up the apparent reasons were that (1) the male was unfavorably orientated with respect to the "courted" female (e.g., she was swimming away from him), (2) the male was still partially in juvenal or "eclipse" plumage and thus probably had a high response threshold, or rarely, (3) the male was physically prevented from Nod-swimming by the presence of several other birds directly in front of him.

Variations in display intensity were evident in all of the displays. For example, low intensity performances of all three major displays often lacked the whistle that normally is associated with all of them. This was particularly true during the first few weeks of display when many birds were still molting into nuptial plumage and also during the last weeks of display in April. Of the three major displays, the Down-up appears to be the most variable in intensity, judging from inspection of motion picture film. That is, the "Down" phase varied from only a very slight downward body inclination to one in which the whole forepart of the body was submerged. Variations in the length of time required to complete a display did not appear to be great, with the notable exception of Nod-swimming, in which the female's orientation had a profound effect on this display's length.

All of the above examples of variation seem explainable by quantitative

TABLE 3

RECORDED BOUTS OF BLACK DUCK DISPLAY COMBINATIONS

		Males Performing Head-up-tail-up Display					
		0	1	2	3	4	5
Males Performing Down-up Display	0		152 / (107)	59 / (30)	23 / (8)	1 / (2)	1 / (0)
	1	61 / (107)	35 / (60)	10 / (24)	4 / (9)	1 / (3)	
	2	27 / (30)	14 / (24)	5 / (14)	0 / (6)		
	2	17 / (8)	11 / (9)	5 / (6)			
	4	17 / (12)	5 / (3)				
	5	8 / (0)					

variations in stimuli strength and response thresholds of individual birds. Evidence for genetic variation within the total population was possibly indicated by the small percentage of abnormal displays seen. For example, although the display which Lorenz (1951) termed "Bridling" normally occurs in the male Mallard only after copulation, it was observed to be intercalated between the Head-up-tail-up and Nod-swimming on three occasions out of the total 625 Head-up-tail-up and Nod-swimming combinations recorded. In the Black Duck this variation was recorded twice out of the 479 such combinations. In addition, an independent Bridling followed by Nod-swimming was observed twice in the Mallard and not once in the Black Duck. Finally, an isolated Bridling movement was observed once in the Mallard. It is of interest that Bridling normally occurs in these same display combinations in a few closely related species such as *Anas castanea* (Lorenz, 1951–1953), which suggests that this might be an ancestral mallard condition which is occasionally expressed in certain genetic recombinations or mutant individuals.

Hybrid Behavior and Mallard-Black Duck Interaction.—Wild hybrids between Mallards and Black Ducks are relatively common in the Ithaca area, and repeated counts of wild Black Duck flocks suggest that roughly 3 per cent of the males exhibit rather obvious hybrid ancestry. Hybrid incidence is considerably higher toward the western edge of the Black Duck's range (Johns-

gard, 1959), but they occurred in sufficient numbers in the area of study to allow certain observations of behavior.

Since no qualitative differences were observed in the behavior of the parental forms, it is not surprising that hybrids exhibited no noticeable deviations in their sexual displays. Hybrids also exhibited no greater or lesser frequency of display, although I do not have sufficient data to demonstrate this statistically. In short, hybrids displayed among courting groups of both parental forms, but those which showed a predominance of Mallard or Black Duck characteristics usually were to be found displaying with that form. All of the male displays observed in Mallards and Black Ducks were seen in hybrids and under the same conditions.

Display interaction between Mallards and Black Ducks is an important consideration when trying to determine the degree to which speciation has progressed and isolating mechanisms have evolved. Such interaction did occasionally occur in wild flocks, although courting groups were usually composed entirely of one form or the other. A few observations of Black Duck males displaying with Mallards were obtained, and since they have a bearing on the question of whether male Mallards and Black Ducks are responding to the same female stimuli when they perform the same displays, they will be mentioned here. For example, in the four instances where Black Duck males were observed to perform Down-ups simultaneously with male Mallard displays, these Mallard displays included two Grunt-whistles, three Head-up-tail-ups, and four Down-ups. Although the records are admittedly scanty they do suggest that male Mallards and Black Ducks are responding to the same stimuli when they perform the same displays, and that a female Mallard provides no less of a stimulus than does a female Black Duck under the same conditions, since the Black Duck displays were of equal or higher intensity than the male Mallard displays which were performed simultaneously.

Relationship of Plumage Pattern to Mating Success.—If Darwin's ideas concerning the importance of sexual selection in mating success are correct, it follows that the sexually dimorphic plumage of the male Mallard must be related to its chances of obtaining a mate. It should also be true that males with abnormal or subdued coloration would have less chance of obtaining a mate. Thus, hybrids or Black Duck males presumably would be selected against in a competition for female Mallard mates. Although no information relative to this possibility was obtained on wild birds, some observations bearing on this problem were obtained on the semi-tame ducks at Stewart Park. Here, in addition to the approximately 100 normally plumaged drakes, there were five birds which deviated markedly from the typical male Mallard plumage pattern. These deviations are rather commonly found mutations in domesti-

cated Mallard flocks, such as birds lacking the chestnut breast, having reddish flanks, etc. To test the possibility that such males are less likely to obtain mates because of these aberrations in their plumage signal characters, records were kept on the frequency with which these males displayed relative to the normal "wild type" males. These observations were begun in February, after most birds were already paired and the remaining unattached males were competing for the relatively few unpaired females. The results of these counts are presented in Table 4. It will be seen that the small percentage of drakes possessing abnormal coloration contributed a relatively large percentage of the total male displays recorded during the period of observation, and that they, therefore, were being forced to compete more strongly for mates than were the wild type males. This was most marked during February and March, before mated pairs had begun to break away from the main flock to begin nesting activities. However, by April most pairs had dispersed, leaving only the excess males and a very few females. During that month the aberrant males contributed approximately the expected percentage of displays, since nearly all the other remaining males were also still unpaired. So far as

TABLE 4

FREQUENCY OF DISPLAYS IN WILD-TYPE AND ABERRANT MALE MALLARDS

	Feb.	Mar.	Apr.	Total
Grunt-whistles				
by wild-type males	69	79	60	208
by aberrant males	17	23	14	54
Total displays	86	102	74	262
Head-up-tail-ups				
by wild-type males	40	31	33	104
by aberrant males	6	10	13	29
Total displays	46	41	46	133
Down-ups				
by wild-type males	117	82	50	249
by aberrant males	21	19	9	49
Total displays	138	101	59	298
Combined displays				
by wild-type males	226	192	143	561
by aberrant males	44	52	36	132
Total displays	270	244	179	693
Per cent by aberrant males	16.3	21.3	20.0	19.0
Total wild-type males present	95	76	22	64 (Ave.)
Total aberrant males present	5	5	5	5
Per cent of males aberrant	5.0	6.2	18.5	7.2
Per cent excess aberrant male displays	11.3*	15.1*	1.5	12.8*

*Significant at .01 level.

could be determined, none of these abnormally plumaged males obtained mates. It may be concluded therefore that females are indeed "selecting" normal plumaged birds in preference to these mutants, and that selection for the typical Mallard-type male plumage pattern is probably in operation.

Discussion

The data presented above have pointed out two distinct differences in the displays of the Mallard and the Black Duck. These are (1) the markedly lower male response threshold in Black Ducks in comparison with Mallards, as indicated by the mean number of males responding simultaneously (see Table 1 and Fig. 4), and (2) the somewhat more specific responses of male Black Ducks over Mallards during simultaneous, multiple male displays, especially in those involving five or more birds (see Figs. 5 and 6).

Although these differences are not nearly so great as one might expect to find in two distinct species, they are nevertheless significant from both a statistical and an evolutionary standpoint. It seems entirely reasonable to assume that the Black Duck has been forced to evolve a more specific and sensitive species-recognition system in the form of displays than has the Mallard, as a result of the former's lack of special male plumage characters. Such male plumage patterns as are found in the Mallard would presumably render less necessary a precise behavioral species-recognition system, since these distinctive patterns would probably carry the major burden of signal specificity. In areas where selection for species recognition is reduced (as on oceanic islands where only a single species of *Anas* occurs), male plumage dimorphism is rapidly lost, since selection for concealing coloration is apparently greater than are any pressures for retaining male dimorphism through sexual selection alone. No detailed behavioral studies of any of these isolated populations such as the Hawaiian Mallard (*Anas platyrhynchos wyvilliana*) or the Laysan Mallard (*A. p. laysanensis*) have yet been undertaken, but it would be most interesting to determine whether the behavioral specificity of these forms has undergone a deterioration similar to that of the male plumage patterns because of the absence of a need for a precise species-recognition system.*

In theory, assuming a mixed population of male Mallards and Black Ducks competing for a limited number of female mates, sexual selection would seem to favor the Mallard because of the strong visual stimulus provided by its elaborate plumage, which might possibly provide a kind of "super-normal stimulus" to female Black Ducks. However, this advantage might be counteracted by the male Black Duck's lower, and apparently more specific display threshold, which would provide a potentially more sensitive and effective

* Recent observations at the Wildfowl Trust on these and other island races indicate that this supposition is true.

signal system to females. Such a mechanism might explain the occurrence of male Black Ducks found paired with female Mallards in the wild (Johnsgard, 1959). I have recorded or have been informed of only six such pairs and only three pairs of the male Mallard and female Black Duck type. Additional comments on the possible importance of male plumage patterns, male displays, and female "Releasing Mechanisms" in species-recognition systems are presented by Dilger and Johnsgard (1959).

The behavioral differences encountered between the Mallard and the Black Duck might also be of significance in the general question of the evolution of behavioral isolating mechanisms. It seems to be a general truth that, in the genus *Anas* at least, behavioral differences among distinct but closely related species tend to be relatively minor although male plumage patterns may vary markedly. This also appears to be true in other avian groups (Hinde, 1959). Thus, although several species of *Anas* possess the Grunt-whistle, the optical and auditory stimuli produced by its performance vary greatly in different species as a result of differences imposed by plumage patterns, vocalizations, and variations in body size and form. In addition, variations undoubtedly also occur in the relative frequency of performance of this display and the female stimulus required to elicit it. It might be possible that one of the first stages in speciation is the evolution of threshold differences (or "tendency" differences, see Hinde, 1959) determining the performance of different male displays in isolated populations. Concommitant with these male variations, the females must simultaneously evolve variations in stimulus thresholds so that the male and female stimulus-response systems remain in synchrony (Dilger and Johnsgard, 1959). Conceivably, two such isolated populations might have gradually evolved such quantitative (or even qualitative) differences in these stimulus-response systems that by the time they acheive secondary contact the differences in the two systems are of such a magnitude that a stimulus presented by the females (or males) of one form invariably results in the incorrect response by individuals of the opposite sex in the other form. In such a way behavioral isolating mechanisms might be evolved, which could be strengthened by the evolution of male plumage differences or other morphological (and ecological) variations through selection of random mutations or by reinforcement of morphological, behavioral, and other differences through selection against disadvantageous hybridization (Sibley, 1957).

Conclusions

1. Male Mallards and Black Ducks tend to react independently and rather specifically to female stimuli.

2. Thresholds of male Mallard and Black Duck display responses vary seasonally, as apparently also do female stimulus thresholds.

3. The three major male sexual displays studied have the same hierarchy of reaction intensities in both the Mallard and the Black Duck.

4. No qualitative differences between male Mallard and male Black Duck displays were found.

5. Male Black Ducks have a distinctly lower threshold of display response, and apparently a somewhat more specific response, than do male Mallards.

6. These last two quantitative differences in two forms are believed to be related to the lack of male plumage dimorphism in the Black Duck, which probably must be compensated for by a more sensitive and specific sexual- and species-recognition mechanism than is needed by the Mallard, where male plumage characteristics alone can effect sexual and species recognition.

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DEPARTMENT OF CONSERVATION, CORNELL UNIVERSITY, ITHACA, N. Y., JULY 8, 1959

REQUESTS FOR INFORMATION

The reproductive biology of Cardinals has been under study in this area for six years. I wish now to compare local data with data from elsewhere in the species' range. For this purpose I am soliciting information on extreme dates of nesting, frequency of nests in different months, clutch-size with dates, nesting sites, and extent of cover available for first nests. Details of the study will be supplied to anyone interested in assisting me.—*D. M. Scott, Department of Zoology, University of Western Ontario, London, Ontario, Canada.*

As part of the preparation for a monograph on the Carolina Parakeet, I plan to make a census of extant specimens. I shall write to larger museums, but would greatly appreciate information on specimens of whatever nature in private hands or small collections.—*Daniel McKinley, Salem College, Winston-Salem, N. C.*

FOREST BIRD COMMUNITIES IN THE APOSTLE ISLANDS OF WISCONSIN

BY EDWARD BEALS

In the past few years more ecologists have become aware that the description of plant and animal communities as discrete ecological units is an oversimplification of community relationships. Among botanists, Gleason (1926) has proposed that, inasmuch as each plant species has environmental requirements different from those of every other species, the classification of plant communities into separate and distinct associations is inadequate. Following this individualistic concept, many phytosociologists have developed vegetational gradients based either on measurement of environmental factors (e.g., Ramensky, 1930; Whittaker, 1956) or on a direct analysis of the vegetation itself (e.g., Curtis and McIntosh, 1951; Brown and Curtis, 1952; Goodall, 1954; Horikawa and Okutomi, 1955; Bray and Curtis, 1957). Animal ecologists have also used community gradients in studies of insects (Whittaker, 1952; Kato *et al.*, 1955), copepods (Whittaker and Fairbanks, 1958), and birds (Bond, 1957).

Because different bird species seldom if ever coincide in their ecological distributions, no discrete communities can be clearly defined except where there are sharp changes of environment. Therefore the present paper describes the bird populations within the forests of the Apostle Islands in Lake Superior in terms of a community gradient, relating these bird communities to their environmental framework. Scientific names of plants follow Gleason (1952).

Acknowledgments

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Description of the Region

The Apostle Islands are situated in Lake Superior at the northernmost tip of Wisconsin. There are 22 islands in the group, most of which are low, rising no more than 50 to 75 feet above the lake level. Oak Island is an exception, rising nearly 500 feet. In size they range from a few acres to over 20 square miles. The largest, Madeline, has been most subjected to human disturbance,

and it is the only island that supports a year-round human population. Several others have summer cabins.

The summer climate is remarkably cool, with a mean July temperature of 65°F. It is characterized by a high proportion of rainy days.

The islands lie in the hemlock–white pine–northern hardwoods region of Braun (1950). Extensive trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) forests occur on some of the islands, where fire or logging has destroyed the original vegetation. Only a few forests of red, white, and jack pines (*Pinus resinosa*, *P. strobus*, and *P. banksiana*) occur on the islands. Red oak (*Quercus rubra*) forests may occur on higher locations. The predominant undisturbed vegetation consists of one or more of the following tree species: sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), white cedar (*Thuja occidentalis*), and hemlock (*Tsuga canadensis*). Dense populations of white-tailed deer (*Odocoileus virginianus*) have had a profound effect on the vegetation on some islands; elsewhere deer do not occur at all. Fields have been cleared on Madeline and Sand islands, and open bogs occur spottily, but the bird populations of these particular vegetation types were not studied in detail. For a general descriptive account of the birds of this region in all habitats see Beals (1958*a*).

Field Methods

In comparing communities it is desirable to study as many of them as possible in order to obtain more adequate information regarding the differences among communities. Therefore a rapid sample count method was used to census the birds in this study, somewhat similar to the methods used by Dambach and Good (1940) and by Bond (1957).

The sites were selected on the basis of previous studies of the vegetation (Beals, 1958*b*). Since much of the forested land is continuous on the islands, distinct stands of vegetation were seldom found. Areas of 20 to 40 acres, homogeneous in their vegetation at least for the dominant trees (Beals, 1958*b*), were selected for the vegetational survey. These stands had indistinct boundaries, except when bordering the lake, a bog, or a clearing.

The bird poplations of 24 stands were sampled in late June and early July of 1957 and in late June of 1958. The breeding season apparently reaches a peak around the end of June. Stands were usually sampled between five and eight o'clock in the morning, but on chilly mornings birds were active until nine or later.

A sample count was made by entering a given stand for about 100 yards, standing at a point for five minutes, recording the number and kinds of birds heard or seen, and then proceeding to another point within the stand 150 paces away (125 to 135 yards) and standing for another five minutes. This was

repeated until ten points in the stand had been sampled. Birds seen flying high overhead, such as ducks and gulls, were not counted; those flying close to the canopy if not in it, including Chimney Swifts, Blue Jays, Common Ravens, Common Crows, and Cedar Waxwings, were included.

For each species, frequency (the number of points at which the species was observed) and density (the total number of individuals observed) were recorded in all the stands sampled. For loud-voiced birds or wanderers the same individual may have been observed at more than one point, so that frequency could have a higher value than density. An attempt was made not to count the same individual twice in the recording of density.

A method similar to this one has been checked for its accuracy in southern Wisconsin by Bond (1957), and he considered it a reasonable estimate of the relative values of bird populations. In this study one stand was sampled three times within one week, and the lowest similarity between any two of the samples was 84.9 per cent. (The method of calculating this similarity is described later.) This suggests that results from the sample count method are fairly constant. If one assumes that individuals of a given species of bird act similarly in different stands, in respect to their singing behavior and motor activity, the sampling method used here appears to be valid for a comparative study such as this one.

The sampling of a stand by this method took between one and one and one-half hours, so that if stands were close together, two could be sampled in a morning. However, most stands were rather far apart, and the mode of transportation (by foot or by boat) was slow, so that usually only one stand was sampled in a day.

Statistical Methods

Data from the field include two values for each species in each stand—the frequency and the density described above. These data are considered comparable for a given species between stands, assuming that the species does not differ appreciably in its conspicuousness from stand to stand. But comparisons between species within a given stand were made very cautiously, since species do differ markedly in their conspicuousness. Proportion of time spent singing, loudness of song or call notes, and amount of motor activity, all affect the observations recorded by the sample-count method. The density figure obtained by this sampling method might be distinguished from absolute and relative density figures as an "audiovisual" density index, which is presumed to bear some relationship to the absolute density for each species. Colquhoun (1941) developed coefficients of relative conspicuousness for various European species, which could theoretically be used in estimates of actual density. However, no valid estimate of the number of birds per fixed unit area is pos-

sible in this study, since no such "conspicuousness" coefficients are known and since the area of each sample is indeterminate. I have assumed that an estimate of absolute density is not necessary for comparisons of communities in the manner described below.

A single quantitative value for each species was desired in order to make comparisons between stands, and yet both frequency and density were considered necessary in determining the importance of the species in the community. Several birds observed at one point are considered less important, for example, than the same number of birds scattered throughout the community. The measure of such "importance" used by Bond (1957) was the sum of relative frequency and relative density. However, reducing frequency and density to relative values is not entirely satisfactory since direct comparisons were desired between stands for each species.

An index was obtained by multiplying the density of a species by the square root of its frequency, the product being called a "prominence value." It is to be distinguished from the "importance value," a term which has been used by plant and animal ecologists (Curtis and McIntosh, 1951; Brown and Curtis, 1952; Bond, 1957; and Beals, 1958*b*) to refer to a summation of relative figures, giving a constant value for the sum of all importance values in a stand. The term was first used by Curtis and McIntosh (1951) to denote the sum of relative frequency, relative density, and relative dominance of a tree species.

In determining the prominence value the number of individuals of a species in a stand is the most important figure, while the frequency, a measure of the distribution through the woods, is used to modify the density figure. The square root of the frequency is considered a sufficient modification, so that ten birds found all at one point are about one third as "prominent" as one bird found at each of ten points. By this method also, one bird observed at one point is half as "prominent" as one bird observed at four points. The index admittedly is arbitrary, but it is considered a reasonable quantitative method for describing the prominence of a species in a community.

A two-dimensional ordination of communities was constructed in a manner similar to that described by Bray and Curtis (1957) for plants. The method is based on a coefficient of similarity, calculated as $C = \frac{2w}{a+b}$, where a is the sum of quantitative values (in this case prominence values) of all species in one stand, b is the sum of quantitative values in another stand, and w is the sum of quantitative values the two stands have in common for each species.

To give a simple, hypothetical case, two stands have three species of birds: Stand A has prominence values for species X of 10, for species Y of 63, for species Z of 1; stand B has prominence values for species X of 1, for species Y of 33, for species Z of 36. To find w, the lowest values between

two stands for each species are summed: $w = 1 + 33 + 1 = 35$. Therefore $C = \frac{2 \times 35}{74 + 70} = .486$; Stands A and B have a similarity of 48.6 per cent. The index ranges from zero, if the stands have no species in common, to 1.00 if they are by chance identical—exactly the same species in exactly the same amounts.

Birds with a high prominence value were more important in determining the coefficient of similarity than birds of low prominence. This procedure does involve the weighting of species within a stand; however, this weighting of prominence values no longer implies a comparison of density of birds within the stand. Prominence values were not reduced to relative figures (with a constant sum of 100 per cent) since this might obscure differences between stands for a given species, if the sum of prominence values was very different for the two stands.

A matrix was constructed showing coefficients of similarity for each of the stands with the 23 other stands. The coefficients were totaled for each stand, and the stand with the lowest sum could be considered the stand most different from all the others. It was used as one end of the first or x axis of the ordination. The other end stand of this axis was the stand having the least in common with the first.

Since this ordination attempts to arrange the stands according to their relative dissimilarity, inverse values of the coefficients of similarity were used, subtracting the coefficient from .85. This value was chosen rather than 1.00 because in sampling one stand three times, the coefficients of similarity between the samples were .849, .863, and .907. In other words, two stands with a similarity of .85 or higher should probably be considered essentially identical. Two stands with nothing in common would be 85 units apart (multiplying the inverse by 100). Expressed in these units, the distances between stands will be called *dissimilarity* values.

The length of the axis of an ordination is equal to the dissimilarity of the two reference stands. Each of the other stands is located by drawing arcs representing the dissimilarities from the two ends (Fig. 1). These arcs intersect each other above and below a line drawn between the two reference stands, and the arc intersection is projected onto this axis (Bray and Curtis, 1957). In practice the values of stands along an axis were calculated from a formula derived as follows. Two triangles can be found in Fig. 1, with sides $ex D_a$ and $e(L-x) D_b$, respectively. The hypotenuses are known (dissimilarities from the end stands, D_a and D_b); one side is equal in both triangles (the distance from the axis line to the arc intersection, e); and the sum of the third sides of the two triangles is known (the length of the axis, L). The triangles have the fol-

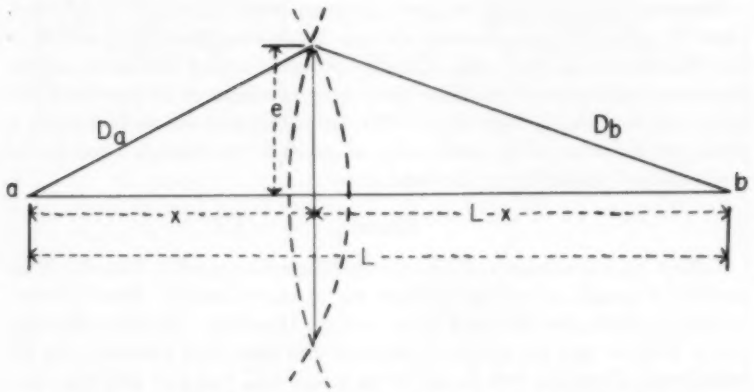

FIG. 1. Demonstration of stand location along an axis of the ordination, by projection of the point of arc intersection; a and b are reference stands, L is the dissimilarity value between the reference stands (the length of the axis), D_a and D_b are dissimilarity values of a given stand from the two reference stands, and x is the location of that stand along the axis.

lowing equations according to the Pythagorean theorem:

$$e^2 + x^2 = D_a^2$$

$$e^2 + (L-x)^2 = D_b^2$$

Subtracting one equation from the other, to eliminate e^2, and solving for x (the value along the axis from Stand A), the working formula results:

$$x = \frac{L^2 + D_a^2 - D_b^2}{2L}$$

Calculation is simplified somewhat by the fact that L is constant for all stands along a given axis.

When all the stands are located along the x axis, there are stands placed close together which in reality are quite dissimilar. Therefore a second or y axis was constructed to separate these. The first reference stand on the y axis was selected on the basis of the highest e value along the x axis (the stand of poorest fit along the first axis). The value of e is calculated as follows: $e^2 = D_a^2 - x^2$. The other end stand is the most dissimilar one to the first end within a distance from the latter, along the x axis, of less than 10 per cent of the total length of the x axis. In this way the second axis approximates a perpendicular relationship to the first. When the two ends were selected and placed the proper distance apart according to their dissimilarity, the other stands were located along the y axis as they were for the x axis. The stands were then plotted on a two-dimensional graph.

Distances between stands on the ordination were calculated as $d_x^2 + d_y^2$, where d_x is the difference between the two stands along the x axis, and d_y is the difference along the y axis. Correlation between these distances and the respective coefficients of similarity for a random sample of 50 interstand distances was remarkably high ($r = -.922$), indicating that the method yields a close approximation of the relationship of stands to one another based on the coefficients of similarity as calculated above.

Results

Table 1 gives a summary of data for the 60 species recorded. Presence is the number of stands out of 24 in which the species occurred. There are two ubiquitous birds, the Red-eyed Vireo and the Ovenbird. The Black-throated Green Warbler and the American Redstart also show high presence. On the other hand, 15 species (one fourth of the total) were found in only one stand each.

Stand abundance is used here as the average audiovisual density of a species for all stands in which that species actually occurred. It is an indication of the densities commonly reached in the habitat of the species. Highest values are achieved by the Ovenbird and Black-throated Green Warbler; among other widespread species, the Hairy Woodpecker, American Redstart, and Solitary Vireo show low stand abundance. Birds reaching highest audiovisual densities in any stand are the Black-throated Green Warbler, Ovenbird, Red-eyed Vireo, White-throated Sparrow, and Least Flycatcher.

The forest types in Table 1 are rough groupings of the stands studied. The pine "type" includes three stands, one dominated by jack pine, one by red pine, and one by white pine. Because these pine forests are so different from one another, the values in the table are followed by letters indicating in which of the three pine stands the species were found. There were four aspen stands, two almost pure trembling aspen, one trembling aspen mixed with much balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), and another dominated by big-toothed aspen (*Populus grandidentata*). There were three white birch–red oak stands. The white birch–yellow birch–white cedar type includes six stands, which contain some of all three species, generally with two of the species dominant. There were three hemlock–yellow birch stands. Of the five sugar maple–yellow birch stands two were almost pure maple.

The distribution of stands within the ordination, each identified as to island, is pictured in Fig. 2; they are clustered toward the lower central portion of the graph, with a few scattered stands to the left, the upper left, and the upper right of this concentration. Fig. 3 shows the distribution of 24 bird species within the ordination, and Fig. 4 shows the distribution of certain tree groups and other vegetational characteristics.

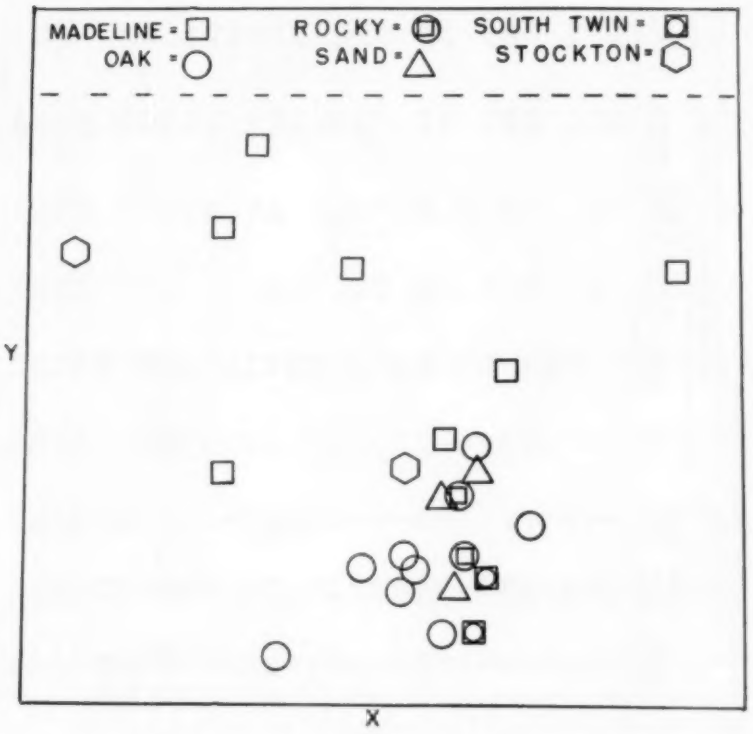

FIG. 2. The distribution of stands within the ordination according to island.

ECOLOGICAL DISTRIBUTION OF SPECIES

The following observations regarding the ecological requirements or preferences of birds were made. The species are divided into four general groups: those occurring mostly with the Black-throated Green Warbler, those occurring mostly with the White-throated Sparrow, those occurring with both, and those occurring with neither. These two reference species are found in high densities in their respective habitats, and yet their prominence values are negatively correlated with each other, significant at the 5 per cent level. Such a division into groups is quite arbitrary; the divisions were made by simple inspection and not in quantitative terms, but the result is a reasonable grouping of species often found together.

TABLE 1

SUMMARY DATA FOR ALL BIRD SPECIES RECORDED

Species	Stand Presence	Stand Abundance	Maximum Density	Average density for six forest types					
				Pines*	Aspens	W. Birch–R. Oak	W. Birch–Y. Birch–W. Cedar	Hemlock–Y. Birch	S. Maple–Y. Birch
Goshawk (*Accipiter gentilis*)	1	2.0	2					0.7	
Sharp-shinned Hawk (*Accipiter striatus*)	1	1.0	1			0.3			
Bald Eagle (*Haliaeetus leucocephalus*)	1	2.0	2						0.4
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	1	1.0	1		0.3				
Long-eared Owl (*Asio otus*)	2	1.0	1	0.3[r]				0.3	
Chimney Swift (*Chaetura pelagica*)	8	2.5	7	0.3[r]			2.0	1.0	2.0
Yellow-shafted Flicker (*Colaptes auratus*)	8	2.0	5		2.0	1.3			0.2
Pileated Woodpecker (*Dryocopus pileatus*)	3	1.7	3		0.3		0.2		
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	5	2.2	5					3.0	0.4
Hairy Woodpecker (*Dendrocopos villosus*)	13	1.8	5		2.0	0.3	0.8	3.7	0.4
Downy Woodpecker (*Dendrocopos pubescens*)	1	1.0	1		0.3				
Black-backed Three-toed Woodpecker (*Picoïdes arcticus*)	1	1.0	1			0.3			
Great Crested Flycatcher (*Myiarchus crinitus*)	5	1.4	3		0.3	0.3	0.5	0.7	
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	2	3.5	5					2.3	
Traill's Flycatcher (*Empidonax traillii*)	1	3.0	3		0.8				
Least Flycatcher (*Empidonax minimus*)	5	11.6	27		4.5			13.0	0.4
Eastern Wood Pewee (*Contopus virens*)	14	6.9	16	4.3[r w]	4.0	0.8	2.2	6.3	5.8
Blue Jay (*Cyanocitta cristata*)	15	2.9	8	3.0[j w]	2.8		1.8	1.0	2.4
Common Raven (*Corvus corax*)	5	1.8	3	0.7[r]	0.8				0.8
Common Crow (*Corvus brachyrhynchos*)	5	2.8	4	0.7[w]			0.7		0.4
Black-capped Chickadee (*Parus atricapillus*)	9	3.2	6	0.3[w]	0.8		1.5	3.3	0.8
White-breasted Nuthatch (*Sitta carolinensis*)	4	3.0	5	1.7[w]	0.8			1.3	
Red-breasted Nuthatch (*Sitta canadensis*)	4	2.3	4	2.0[r w]	0.3			0.7	
Brown Creeper (*Certhia familiaris*)	3	1.0	1				0.2	0.3	0.2
House Wren (*Troglodytes aedon*)	2	4.0	5		2.0				
Robin (*Turdus migratorius*)	8	2.4	4	1.3[j w]	2.0	1.0	0.5	0.3	
Hermit Thrush (*Hylocichla guttata*)	5	3.6	9	3.0[r]	1.0	1.0	0.2		0.2
Swainson's Thrush (*Hylocichla ustulata*)	15	4.7	10	2.0[r]	1.8	3.0	4.8	1.3	3.7
Veery (*Hylocichla fuscescens*)	12	3.3	18	0.3[j]	2.5	9.0		0.3	

* j = jack pine stand, r = red pine stand, w = white pine stand.

TABLE 1 (continued)

Species	Stand Presence	Stand Abundance	Maximum Density	Average density for six forest types: Pines*	Aspens	W. Birch–R. Oak	W. Birch–Y. Birch–W. Cedar	Hemlock–Y. Birch	S. Maple–Y. Birch
Golden-crowned Kinglet (*Regulus satrapa*)	4	1.3	2	1.0[jw]	0.3			0.8	
Cedar Waxwing (*Bombycilla cedrorum*)	4	3.8	10				1.8	1.3	
Solitary Vireo (*Vireo solitarius*)	16	2.8	10	4.0[rw]	1.2	1.3	1.0	2.7	2.0
Red-eyed Vireo (*Vireo olivaceus*)	24	17.7	34	10.7[jrw]	12.8	23.3	23.8	7.3	21.2
Warbling Vireo (*Vireo gilvus*)	1	2.0	2					0.7	
Black-and-white Warbler (*Mniotilta varia*)	14	4.6	10		2.3	6.3	2.7	0.7	3.8
Tennessee Warbler (*Vermivora peregrina*)	1	1.0	1			0.3			
Nashville Warbler (*Vermivora ruficapilla*)	5	2.6	8	4.0[rw]			0.2		0.4
Parula Warbler (*Parula americana*)	9	3.4	5				3.0	1.3	1.8
Magnolia Warbler (*Dendroica magnolia*)	2	4.0	6		0.5				1.2
Black-throated Blue Warbler (*Dendroica caerulescens*)	4	2.5	4				0.7	0.7	0.8
Black-throated Green Warbler (*Dendroica virens*)	22	21.8	43	16.3[jrw]	7.8	11.7	29.5	13.3	20.7
Blackburnian Warbler (*Dendroica fusca*)	7	3.7	7	3.3[rw]			1.3	1.3	0.4
Chestnut-sided Warbler (*Dendroica pensylvanica*)	7	2.6	5		0.3	1.7	1.0		1.5
Pine Warbler (*Dendroica pinus*)	1	4.0	4	1.3[r]					
Ovenbird (*Seiurus aurocapillus*)	24	23.6	41	24.0[jrw]	18.8	33.3	19.7	18.3	29.2
Connecticut Warbler (*Oporornis agilis*)	1	1.0	1		0.3				
Mourning Warbler (*Oporornis philadelphia*)	2	12.0	16		6.0				
Yellowthroat (*Geothlypis trichas*)	3	1.7	3		1.0			0.3	
Canada Warbler (*Wilsonia canadensis*)	7	6.1	13			6.0	1.3	4.3	0.8
American Redstart (*Setophaga ruticilla*)	18	2.7	6	3.7[jrw]	0.5	3.3	2.2	0.3	1.8
Baltimore Oriole (*Icterus galbula*)	2	1.0	1	0.3[r]	0.3				
Brown-headed Cowbird (*Molothrus ater*)	4	2.3	3		1.3	1.0		0.3	
Scarlet Tanager (*Piranga olivacea*)	6	2.3	4	0.7[j]		3.0	0.3	1.0	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	4	1.5	2		0.5		0.2	0.3	0.4
Indigo Bunting (*Passerina cyanea*)	1	1.0	1		0.3				
Purple Finch (*Carpodacus purpureus*)	5	1.8	5	0.3[r]	0.3		0.8	0.3	0.2
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	1	1.0	1		0.3				
Chipping Sparrow (*Spizella passerina*)	1	2.0	2	0.7[r]					
White-throated Sparrow (*Zonotrichia albicollis*)	5	15.8	29	1.0[r]	18.8		0.2		
Song Sparrow (*Melospiza melodia*)	4	6.8	11	1.3[r]	5.8				

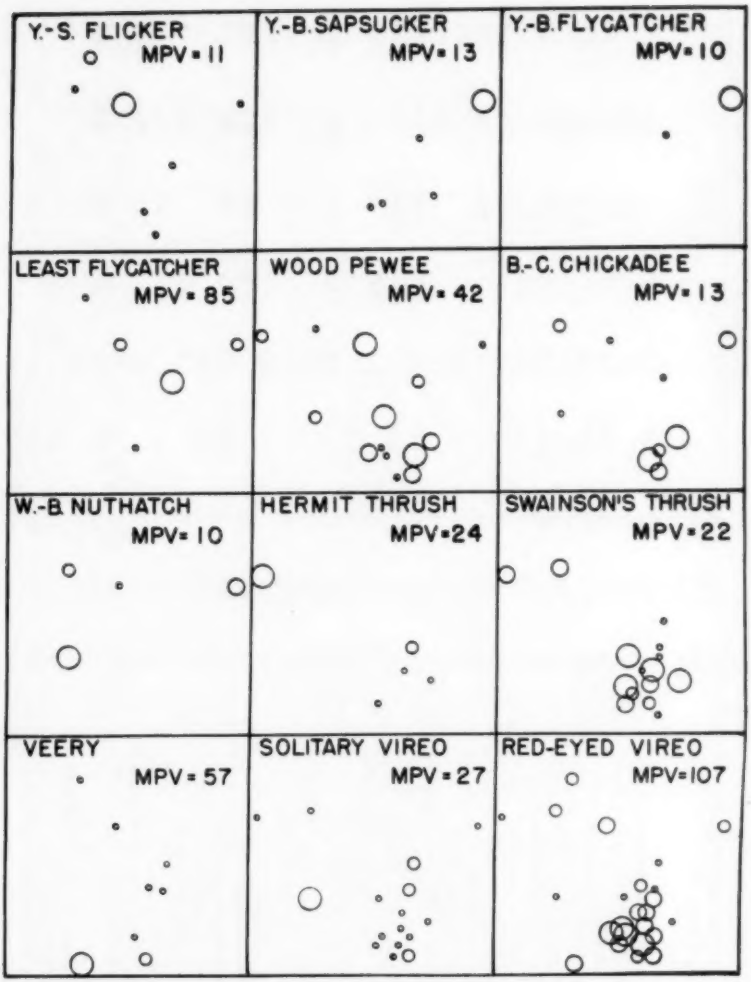

FIG. 3. The distribution of 24 bird species within the ordination. Sizes of circles represent four equal segments of the range of prominence values, based on the maximum prominence value (MPV), of each species.

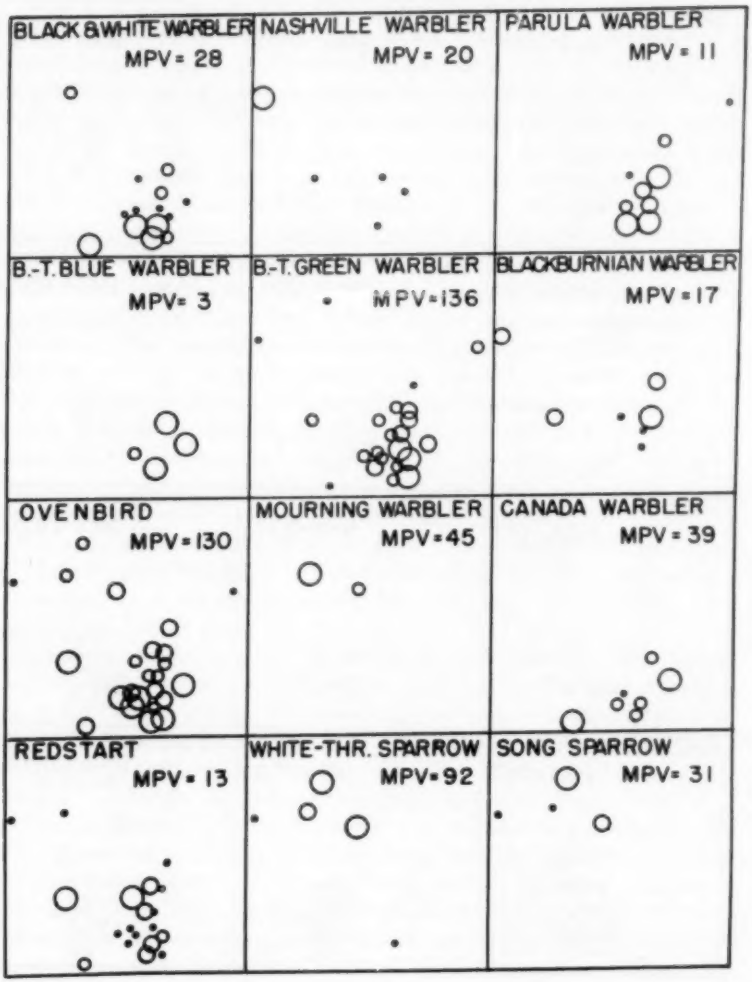

FIG. 3. (Continued)

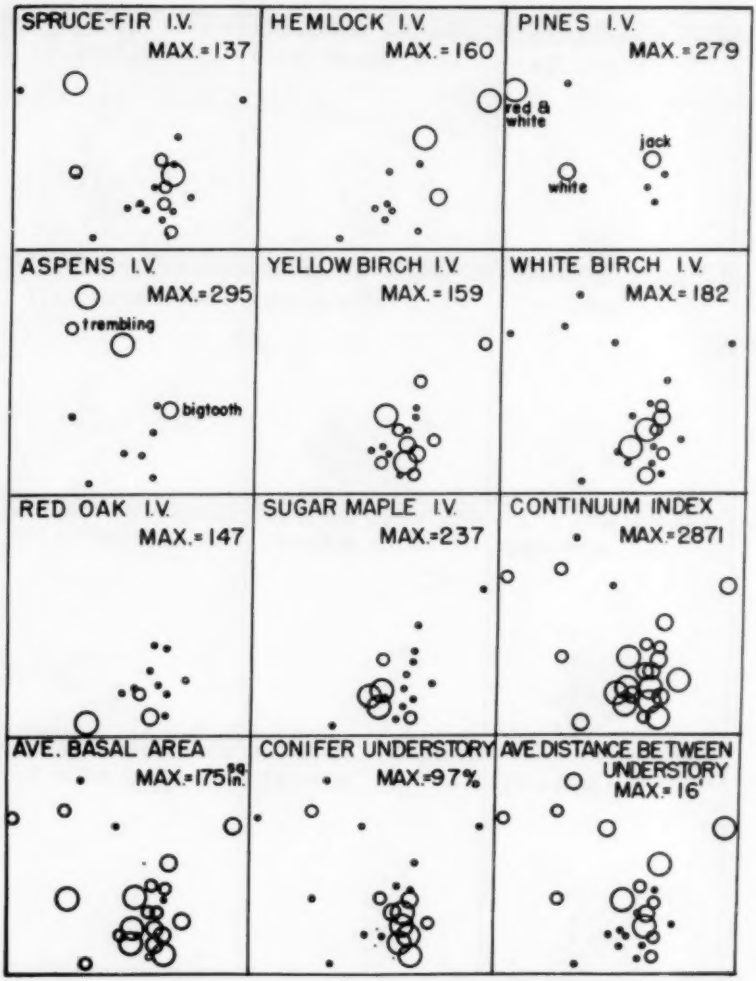

FIG. 4. Distribution of tree species and other vegetational factors within the ordination. Sizes of circles correspond to four equal segments of the range of quantitative values used, based on the maximum value as indicated (I.V. = importance value). For stands where aspens or pines are dominant, the more important species of aspen or pine are named. The dots in the conifer understory block indicate stands with no conifer understory.

Regression was tested in some cases between the species and certain environmental factors. However, most birds respond to a complex of factors, and it seldom happens that a significant value is obtained from an isolated factor. Otherwise the data only suggest trends in the distributions of species. Factors studied were taken from Beals (1958*b*) and included the following: importance values of pines, hemlock, sugar maple, aspens, spruce–fir, white birch, yellow birch, red oak, white cedar, etc.; average basal area of trees, trees per acre, trees at least 10 inches dbh per acre, trees at least 20 inches dbh per acre, total basal area per acre; average distance between stems of woody understory (1 to 7 feet high); relative amount of conifer and understory, etc. One vegetational factor referred to is the continuum index, described for this region by Brown and Curtis (1952). This is based on the importance of trees ranked according to their association with sugar maple at one end and jack pine at the other. A low value (minimum possible, 300) indicates a pioneer forest, and a very high value (maximum possible, 3000) indicates climax vegetation. The values for stands in this study ranged from 614 (aspens) to 2871 (sugar maple forest). See Brown and Curtis (1952) for the method used. This index was tested by correlation coefficient since it is not itself a controlling factor but only an expression of many possible controlling factors.

Birds whose distributions are pictured in Fig. 3 are marked with an asterisk (*) in paragraphs that follow. Those species which occurred in only one or a few stands are mostly just listed, and the reader may refer to Table 1 for vegetational data on them.

Species associated largely with White-throated Sparrow.—The Yellow-shafted Flicker* was widely distributed in small numbers but reached greatest prominence among aspens. This association with aspen coincides with Kendeigh's findings (1948) in lower Michigan and those of Adams (1909) on Isle Royale in northern Lake Superior. Elsewhere it is usually found in relatively pioneer forests also (Odum, 1950; Kendeigh, 1946; Bond, 1957).

House Wrens and Mourning Warblers* were confined to aspen stands, and Yellowthroats were nearly as restricted. Song Sparrows* and White-throated Sparrows* both showed highly significant positive regression with aspen importance values, and a highly significant negative correlation with the continuum index. In other words, these birds all seem to prefer pioneer forests of aspen and to some extent pine. Other studies confirm this preference for pioneer vegetation (Kendeigh, 1946, for Song Sparrow, House Wren, and Yellowthroat; Kendeigh, 1948, for Mourning Warbler and White-throated Sparrow; Stewart and Aldrich, 1949, for Mourning Warbler; and Odum, 1950, for Song Sparrow).

The Veery* was found in greatest numbers in both aspen and red oak forests, especially where understory was densest. In other studies Veeries have

been found to be partial to deciduous forest (Kendeigh, 1948; Stewart and Aldrich, 1949). Kendeigh (1945, 1946) reported a preference for late shrub or early tree stages of succession in New York, and McCreary (1909) considered it characteristic of birch–aspen forests on Isle Royale. On the other hand, Odum (1950) found it most abundant in mature oak forest on the highlands of North Carolina. From the present data, both habitats are apparently used in northern Wisconsin.

Additional but uncommon species in this group are the Black-billed Cuckoo, Downy Woodpecker, Traill's Flycatcher, Connecticut Warbler, Indigo Bunting, and Rufous-sided Towhee.

Species associated largely with Black-throated Green Warbler.—The Chimney Swift occurred widely but seemed to prefer forests with many large trees, and with a high continuum index. The Pileated Woodpecker shows some partiality to white cedar. Other workers (Kendeigh, 1946, 1948; Stewart and Aldrich, 1949) have recorded it in mature conifer–hardwoods, and Kendeigh (1948) recorded it also in cedar–fir forest in Michigan. Blackwelder (1909), working in northwest Michigan, reported a preference by this species for edges between fir–cedar swamps and hardwood–hemlock forests. On the other hand, the Yellow-bellied Sapsucker* is found where hemlocks grow, as is the Yellow-bellied Flycatcher.*

Widely distributed in small numbers are the following: the Great Crested Flycatcher, especially where trees are close together; Common Crow; Black-capped Chickadee,* which shows some affinity for yellow birch stands; Solitary Vireo,* which prefers forests with larger trees apparently; and American Redstart,* which reached high densities in two pine stands and one birch–maple stand. The Scarlet Tanager is usually found in fairly dense forests.

The Red-breasted Nuthatch is restricted mostly to pine (except one hemlock stand), and the White-breasted Nuthatch* is also most common in pine and hemlock, with smaller numbers in fir and aspen stands. In Kendeigh's Michigan study (1948) the Redbreast was more common in cedar–fir than in pine, while in New York (Kendeigh, 1946) the Whitebreast showed some preference for mixed forests dominated by hemlock. The Golden-crowned Kinglet was found in stands containing hemlock, fir, and pine. Observations in this study agree with Bent's experience (1949) that this species prefers more open forests with scattered second-growth spruce (or fir) trees.

The Parula Warbler* is found in forests with a rather high continuum index —possibly because more beard moss (*Usnea*), with which it usually constructs its nest, is available in these undisturbed forests, although this lichen is nowhere abundant. This species' association with climax stands was also found by Stewart and Aldrich (1949) in West Virginia and by Odum (1950)

in North Carolina, while Kendeigh (1948) found the Parula associated with cedar in lower Michigan.

The Black-throated Blue Warbler* occurred sparsely in hemlock, yellow birch, and sugar maple stands. Odum (1950) and Kendeigh (1946) found this bird most common in stands dominated by hemlock. Others (Griscom *et al.*, 1957) reported that it prefers deciduous trees. No preference one way or the other could be determined from the data of this study. Its usual occurrence where yew (*Taxus canadensis*) forms a part of the understory coincides with the reports of Chapman (1907) and Brewster (1938).

In spite of its rather high prominence in sugar maple stands, the Chestnut-sided Warbler shows a tendency to increase where the size of trees is small or the total basal area per acre is low. Where it does occur with maple, the forests are rather open, with a dense understory (due to selective cutting many years ago of red oak in the stands). It reaches highest densities in stands with large amounts of white birch. Stewart and Aldrich (1949), Kendeigh (1946), and Odum (1950) found it had a strong preference for young deciduous growth, and Odum also found it in mature oak stands opened up by chestnut blight.

The Blackburnian Warbler* increases with the increasing importance of conifers in a forest. This agrees with other reports of this species, except that of Brooks (1936), who said that in West Virginia they are quite at home in deciduous second-growth timber. It is more associated with pine in this study than other observers have found.

The Canada Warbler* shows a definite trend to increase as woody understory also increases, with best development in a red oak woods and in a hemlock stand with much fallen timber. While Kendeigh (1946), Stewart and Aldrich (1949), and Odum (1950) reported it in the more climax vegetation, Brooks (1936) said that it is well adapted to deciduous second-growth in his study area in West Virginia, and Stewart and Aldrich (1952) found it most characteristic of cedar–tamarack–ash bogs in Maine.

The Black-throated Green Warbler* is one of the most common species of the forests, and it shows a positive regression with the importance value of yellow birch, significant at the 5 per cent level. The total importance value of spruce, fir, cedar, and hemlock (all the conifers except pines) also tends to correlate with the prominence of this species. There is a lack of preference for pines, quite contrary to observations in New England (Bent, 1953). Allin (in Griscom *et al.*, 1957) observed a similar scarcity in pines north of Lake Superior. In this study, however, it did occur in moderate numbers where pines were mixed with white cedar or fir. This species shows a strong preference for stands with high conifer composition in most other studies (Kendeigh, 1946, 1948; Stewart and Aldrich, 1949), but Brooks (1940) found it

well distributed in northern hardwoods and oak–hickory forests. In the spruce–fir forests on Isle Royale, McCreary (1909) reported this warbler most common where there were many white birch trees among the conifers. In the present study it inhabited areas lacking conifers, but was more common when at least a few conifers (other than pines) were present.

Other species in stands with high values of the Black-throated Green Warbler were the Goshawk, Sharp-shinned Hawk, Bald Eagle, Black-backed Three-toed Woodpecker, Brown Creeper, Cedar Waxwing, Warbling Vireo, Tennessee Warbler, Magnolia Warbler, and Rose-breasted Grosbeak.

Species associated with both reference species.—These included the ubiquitous species and a few others whose environmental requirements, though narrow, apparently cut across those of the two reference species. For instance, the Long-eared Owl was found in a pine stand and a hemlock stand, both of which had some large coniferous trees.

Hairy Woodpeckers were found most prominently in both aspen and hemlock stands but were widely distributed in small numbers, except in the most xeric forests (pine and red oak). In southern Wisconsin Bond (1957) found this woodpecker more common in mesic stands, with sugar maple dominant, than in xeric and intermediate stands, where oaks were dominant. Kendeigh (1948) in Michigan found it in cedar, fir, and aspen types, and other studies (Sutton, 1928; Kendeigh, 1946; Stewart and Aldrich, 1949; Odum, 1950) show it distributed in mesic to wet forests whether pioneer or climax.

The Least Flycatcher* also inhabited aspen and hemlock forests. Two environmental factors were common to the four stands occupied by this bird: very poorly drained soil and mostly deciduous understory. Kendeigh (1948) recorded it in aspen–red maple, cedar–fir, and especially beech–maple–pine woodland.

Wood Pewees* were widely distributed and show little pattern on the ordination. Bond (1957) found a similar lack of patterning in southern Wisconsin for the pewee. With the exception of one aspen stand in which the prominence of this species was high, the size of trees seemed to influence the density of pewees, areas of larger trees being preferred. Kendeigh (1948) in his Michigan studies showed two peaks of population density, one in pine–aspen and one in beech–maple–pine, which correspond somewhat to the results of this study.

Blue Jays and Common Ravens are both scattered over the ordination, and no vegetational characteristics could be pinpointed. Since their territories are rather large, they undoubtedly cover more than one type of habitat.

The Robin is found in aspen, fir, and jack pine forest types, and shows some preference for areas of smaller trees. In Michigan Kendeigh (1948) found it most abundant in pine–aspen, and rather common also in cedar–aspen, cedar–

fir, and aspen–red maple types. Stewart and Aldrich (1949) reported it most common in a young spruce stand. Most observers agree that relatively pioneer vegetation is preferred.

The Hermit Thrush* reached its maximum density in a pine stand, but otherwise was scattered in small numbers in several types of vegetation. Kendeigh's data (1948) indicate that this bird is most common in pine–aspen forest in lower Michigan, with smaller numbers in aspen–red maple.

Swainson's Thrush* is more widely distributed and shows some trend to increase with increasing continuum index values. Stewart and Aldrich (1949) also found this species best developed in climax (virgin spruce–hardwood) forest. The abundance of this species in the Apostle Islands coincides with McCreary's observations (1906) for the near-by Porcupine Mountains in Michigan.

The Black-and-white Warbler* shows preference for the pure sugar maple forests generally. However, its density apparently increases with increasing density of woody understory and with increasing amount of deciduous understory in particular, both of which were characteristic of some of the maple forests studied. In New York Kendeigh (1946) recorded it in all of his three vegetation types, but in Michigan (1948) he found it most common in cedar–aspen and cedar–fir.

The Red-eyed Vireo* and Ovenbird* are two ubiquitous species. The former tends to increase with increasing importance of white birch. Peet (1909) reported that the Red-eyed Vireo prefers white birch forests on Isle Royale. Bond (1957) found Red-eyed Vireo populations densest in the most mesic stands of his xeric to mesic gradient, and in the Apostle Islands white birch occurs most commonly in mesic to wet-mesic stands. The prominence of the Ovenbird shows significant (5 per cent level) regression with the density of the understory, in contrast to Bent's statement (1953) that it usually nests where underbrush is scanty. Stenger (1958) reported that territory size decreased as density of ground vegetation increased in her studies in Ontario. The several nests found in this study were not located in open situations as generally reported (Bent, 1953), but at the base of a tree seedling or among the low branches of a shrub. It was suggested by Stenger (1958) that the understory density is positively correlated with the food supply, which controls, at least in part, population density.

The Baltimore Oriole, Brown-headed Cowbird, and Purple Finch were not very common and showed little pattern within the ordination.

Species not associated with either reference species.—The Nashville Warbler* was most prominent in two of the pine stands, especially the red pine woodland. It also occurred in a cedar stand (as in Kendeigh's findings, 1948) and in two maple–birch stands, one of which contained cedar. Other species

found in stands with low densities of the reference species were the Pine Warbler and Chipping Sparrow.

Discussion

Most plants respond to the same group of environmental factors (light, water, mineral nutrients, etc.), though each species responds in a different way from other species. But one animal species may respond to quite different factors from another species. The ground-feeding insectivorous bird is affected greatly by the insects on the forest floor, but it is little affected by the foliage insects; an insectivorous bird of the canopy is affected quite oppositely. Bark-feeders are probably independent of either of these factors, and seed-eaters will be distributed, at least in part, according to still another group of factors.

However, these different factors are all directly or indirectly related to one another. The autotrophic plants form the base of the food pyramid and often furnish nesting sites and materials. These plants, as mentioned before, respond generally to the same environmental factors, each in its own way, and are therefore distributed in some sort of pattern. Thus the animals must also be distributed in a pattern, although it may be more complex and less evident. For an example of interrelation of factors, Stenger (1958) stated that territory size of the Ovenbird increases as canopy density increases. She suggested that density and composition of the canopy influence the density of ground vegetation and the quality and quantity of humus, which in turn determine the abundance of invertebrates in the soil. The Ovenbird feeds upon the invertebrates. Apparently, then, the density of Ovenbirds is determined in part by the indirect influence of the canopy.

Most non-biotic factors, such as water and temperature, influence all animals and therefore also contribute to the patterning. The interaction between and within species must also be considered in the environmental complex. The ordination is constructed to represent this complex of environmental factors, and, if the birds are distributed according to an environmental complex, the more or less distinct patterns formed by most species of birds supports the validity of this representation.

Several species of birds, such as the Chimney Swift, Wood Pewee, Swainson's Thrush, Solitary Vireo, and Magnolia Warbler, do not follow distinct patterns in the two-dimensional ordination, indicating that the environmental complex represented by the ordination is not influencing the distribution of these species markedly. Species of low presence, such as the Magnolia Warbler, may exhibit broad tolerance to the environment expressed in the ordination but have very narrow tolerance to certain environmental characteristics unimportant to the bird populations as a whole. If the species has high presence, as do most of those without distinct distribution patterns, the lack of pattern may reflect a general broad tolerance to environmental variation.

It is important to realize that this ordination gives just one approximation of stand similarities according to the information in the matrix of coefficients of similarity, and that other approximations might be constructed by different criteria and techniques, which would be just as valid, or possibly even more valid. Yet the distances in this ordination and the coefficients of similarity from the matrix do show remarkably high negative correlation ($r = -.922$, for a random sample of 50 interpoint distances out of a total of 276). It would be expected that distances from the four reference stands would be correlated with the respective coefficients; however, most of the 50 sample distances were between stands not used in constructing the ordination. If the coefficients of similarity originally used were valid, and if differences in species composition between stands is an index of environmental differences, the number and importance of environmental factors not included in some way in the framework of this ordination is probably very small.

Certain environmental factors form excellent patterns within the ordination (Fig. 4), suggesting that these are important factors in the distribution of the birds. The distinctive patterns of hemlock, pines, aspens, red oak, sugar maple, and per cent of conifer understory in Fig. 4 give evidence that these factors make important contributions to the habitat. The average size of trees forms a less discernible pattern, but there appear to be areas of large trees and areas of small trees on the ordination, which suggest that tree size is an important modifying factor within the larger environmental framework. The lack of pattern for spruce and fir may reflect the important differences of associated tree species. One of the two stands of high spruce–fir importance had trembling aspen and white pine as codominants, the other had white birch and red maple.

To examine further the ecology of these bird populations, a second ordination of the 24 stands was run based on the vegetation itself. The method was exactly the same, except that the coefficients of similarity were derived from the vegetational data (trees, shrubs, and herbs) rather than from the birds. The coefficients had already been calculated for the report on the vegetation of the region (Beals, 1958*b*). A comparison of the ordination by birds and that by plants is shown in Fig. 5. Groups of stands together in both ordinations were outlined, and each group was labeled by the tree species which was common to the entire group in greatest importance. The similarities are striking, and the differences are enlightening. In the plant ordination the hemlock group is set between the sugar maple and yellow birch groups, indicating that the hemlock stands share many plants in common with the other two groups. Note, however, that the bird populations distinguish the hemlock group as quite different so that it is pushed to one side of this ordination. The special distinctiveness of pine and aspen forests is confirmed by this comparison, since these two groups are much more segregated from the other groups by

bird composition than they are by plant composition. The differences between the two ordinations, however, are minor compared with their remarkable similarities, which are good indications of the close relationship between birds and the vegetation.

Furthermore, the general concurrence of the results of this study with those of other investigators in various regions, in regard to vegetation preferences, points up the relatively constant nature of the habitat requirements of most species over their breeding range.

Another biotic factor considered was the effect of deer populations. In spite of the influence of deer on the understory vegetation (Beals, 1958*b*), however, no correlations could be found between the deer pressure (as determined by me) and bird populations.

Geographic factors should also be considered. In Fig. 2 the relation of the islands to the ordination shows definite patterns. In examination of the plant ordination such patterning does not occur, so that vegetation cannot be the cause of the island patterns in Fig. 2. (One exception is Oak Island, the stands on which had a similar grouping on both ordinations. In the plant ordination (Fig. 5) the Oak Island stands include all but one of the sugar maple group, all the red oak group, and the uppermost stand each in the hemlock and fir groups. Their vegetational similarity is probably due to the unique topography of that island, with well-drained, deep soil.)

The Stockton Island maple stand in the bird ordination is pushed toward the Stockton pine stand (Fig. 2), while in regard to vegetation it was quite unrelated, located on the right side of the sugar maple group in Fig. 5, with the pine stand at the extreme left. Also, within the bird ordination the Oak Island hemlock and aspen stands are closer to most of the other Oak Island stands than they are to the other hemlock and aspen stands respectively, although obviously there are indeed great differences in bird populations.

Putting this phenomenon on a quantitative basis, the average coefficient of similarity according to the vegetation was about the same for stands on different islands as it was for stands on the same island (.325 for between-island average, .297 for same-island average), while based on birds the average coefficients for stands on the same islands were higher than the average for stands on different islands (.546 compared with .448). To test the difference, the median test described by Mood (1950) was applied. A distribution-free method was used since the distribution of coefficient values was highly skewed. All coefficients were ranked and the median value found. The number of intra-island values higher and lower than the median, and those for the inter-island values, were set up in a 2×2 contingency table. Chi-square was calculated and was significant at the 5 per cent level. Therefore, local geo-

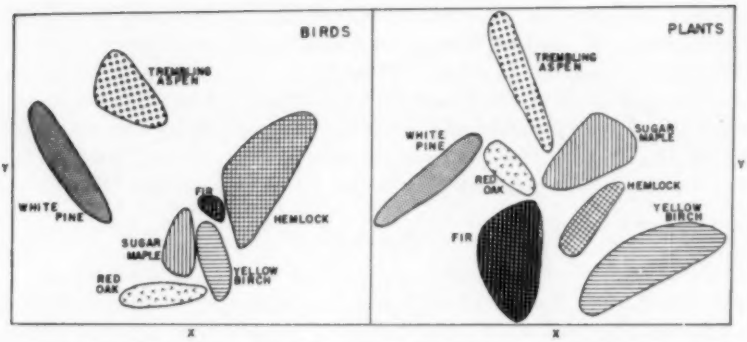

FIG. 5. Comparison of ordination by vegetation and by bird populations. Stands which are grouped together on both ordinations are encircled and are labeled by the tree species which was common to the entire group in greatest importance.

graphic influences apparently do play a role in bird distributions on the Apostle Islands.

The size of islands may have some effect. Fig. 6 shows the relationship of size to the ordination. The two largest islands (Madeline with 13,200 acres and Stockton with 8300) are grouped together. A definite planar gradient can be seen from the smallest island (South Twin, 350 acres) to the next in size (Rocky, 750 acres), to Sand (2900 acres), to Oak (4500 acres), to Stockton and Madeline. Van Tyne (in Hatt *et al.*, 1948) noted that the avifauna on Lake Michigan islands decreased in number of species with decreasing size of the islands, and Lack (1942) reported a similar impoverishment of the bird fauna on small islands around Great Britain. Lack attributes the phenomenon to limitation of habitats, the liability of very small populations of a species to extinction, and the inhibition of migration from other areas by the water. A number of birds in the Apostles were restricted to larger islands (Beals, 1958*a*), such as the birds of prey, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Yellow-shafted Flicker, Yellow-bellied Flycatcher, Veery, and Baltimore Oriole. Diversity of the bird communities (= diversity of habitats?) is definitely correlated with size of islands: the largest island, Madeline, has the lowest average coefficient of similarity between stands (.402), while each progressively smaller island has increasing average similarity (Stockton, .455; Oak, .621; Sand, .704; Rocky, .773; and South Twin, .849). Furthermore, the larger islands tend to have a greater number of species per individual stand (Madeline, 9–26 species per stand; Stockton, 13–21 species; Oak, 9–20 species) than the smaller islands (Sand, 8–17 species; Rocky, 13–16 species; South Twin, 12–15 species), indicating possible avifaunal limitations

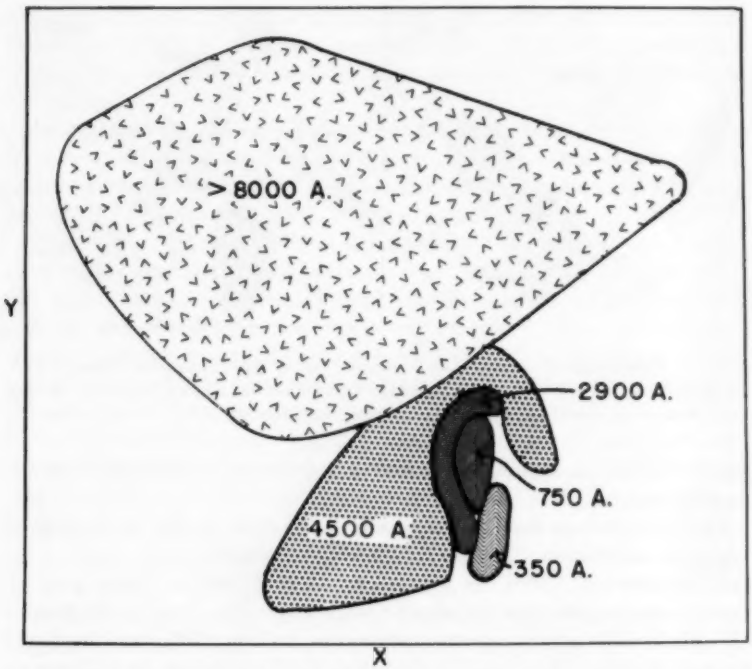

FIG. 6. The pattern of islands in the ordination according to size. Lines surround the stands of an island with the indicated size in acres.

other than lack of habitat variability alone, if one assumes habitat homogeneity in individual stands.

Another geographic influence which may cause added similarity of stands on the same island is related to the behavior of the birds. On the mainland, as population pressure disperses a species into suboptimal environment, individuals may wander considerably until they find suitable habitat, whereas in the island environment large stretches of water (1 to 3 miles or more) may tend to discourage the excess from leaving an island even if all the ideal habitat is occupied. (Unless the birds had some way of knowing that better environment was available beyond the totally unsuitable aquatic habitat, there would probably be little incentive to move out across the water.) Furthermore, the insular topography may accentuate orientation toward the previous breeding or fledging grounds of a bird. This hypothesis would explain the Nashville Warbler's singing in the middle of a birch–maple forest on Stockton, since several hundred yards away was the red pine stand where this species reached

its greatest prominence. And the surprising number of Swainson's Thrushes in that pine stand might itself have been an overflow from the near-by woods of more appropriate habitat. Lack (1942) records several instances of modification of habitat on British islands, which were preceded by increased density in the normal breeding habitat. Additional, more subtle associations of populations with islands—perhaps none of which by itself would be considered significant—may combine to give the increased similarity between stands on an island.

Summary

The bird populations of 24 stands of forest vegetation on the Apostle Islands of Lake Superior were censused by a sample count method. A two-dimensional ordination of the stands was constructed, based on the avifaunal similarities between stands. The ordination represents an environmental complex, within which many bird species are distributed in definite patterns. Certain vegetational characteristics of the stands also show well-developed patterns within the ordination, indicating that they may play an important role in the environmental complex. Aspens, pines, hemlocks, maples, and the relative amount of coniferous understory show excellent patterns. The species of birds observed in the study are discussed in relation to their apparent environmental preferences. Two species found in every stand, the Ovenbird and the Red-eyed Vireo, have broad environmental tolerances. Two others found in at least three fourths of the stands, the Black-throated Green Warbler and the American Redstart, are partial to mature forests, the former especially to birch–hemlock, and the latter to pine as well. In pioneer aspen growth, White-throated Sparrows and Mourning Warblers are most abundant. There are greater similarities between stands on the same island than would be expected from the vegetational variation. The possible influences of island size and of the behavior of birds in relation to island topography are discussed.

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MAY 27, 1959

MALLOPHAGA FROM BIRDS OF NORTH AMERICA

BY RICHARD O. MALCOMSON

SIXTY years have elapsed since a list of Mallophaga with their hosts was made (Kellogg, 1899. Smithsonian Institution Bull. XII:39–100). During this time many new species have been described and new genera have been erected.

The purpose of this paper is to stimulate interest among biologists, including the bird banders, to study the parasites of birds. Almost all birds have parasites, and the bander has a good opportunity to take these without killing the birds, as was done in the past. I would suggest that the bander obtain official sanction (on his banding permit) to carry on this work. He can take these parasites by a very simple delousing process as follows:

Procure an insecticidal powder, pyrethrum for example, a few sheets of white paper and a paper carton. After the bird has been banded, thoroughly dust some of the powder through the feathers, but be careful not to get any powder into the eyes of the birds. Now place the bird on a sheet of white paper and invert the paper carton over it. Allow the bird to flutter around in this enclosure for about five minutes. In the meantime the parasites will have crawled to the tips of the feathers and dropped to the paper. Some of the lice will show movement, but all can be picked up by a small camel hair brush and transferred to a piece of medicinal cotton.

If the bander is not interested in collecting and identifying these parasites for himself, he may record on a slip of paper, the name of the bird, date, place taken and his name as collector. The piece of cotton containing label and specimens may be dropped into an envelope and mailed to some mallophagologist.

The cotton method is the most convenient way to send specimens by mail. On the other hand, if the bander is interested in collecting and identifying his own material, he should put the specimens taken from each bird into separate small vials containing 70 per cent alcohol, to preserve them for some future time. A small slip of paper containing the collector's name, name of the bird, date and place taken should be inserted in the vial. Labels printed with soft lead pencil will be legible indefinitely in 70 per cent alcohol.

To identify the material collected requires a definite process of mounting on microscope slides. Good results may be obtained by the following method:

1. Transfer contents of each vial to a vial of 20 per cent potassium hydroxide for a period of 24 to 48 hours, depending upon the degree of scleritization of the lice.
2. Wash in distilled water 30 minutes.
3. Dehydrate with 35 per cent alcohol for 10 minutes.
4. Place in 50 per cent alcohol for 10 minutes.
5. Place in 70 per cent alcohol for 10 minutes.

6. Place in 85 per cent alcohol plus 15 per cent benzol for 10 minutes.
7. Place in 95 per cent alcohol plus 50 per cent benzol for 10 minutes.
8. Place in absolute alcohol plus 75 per cent benzol for 10 minutes.
9. Place in 100 per cent benzol for 5 minutes.
10. Mount in euparal or a medium with benzol base.
11. Mount in center of slide and cover with 18 mm. round cover slip.

There are more than 2600 recorded species of living Mallophaga, and this paper lists 800 of these species and about 500 species of birds from which they are recorded. I have not recorded any subspecies of Mallophaga. This list of about 800 species probably represents about one fourth of the species yet to be described.

In this paper the birds are listed phylogenetically. Under each bird is listed the scientific names of the Mallophaga known to infest it, as described in the literature of Systematic Entomology. I have followed very closely the classification of Hopkins and Clay in, "A Check List of the Genera and Species of Mallophaga" (1952. British Museum, London).

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Host List with Parasites

Great Tinamou, *Tinamus major*
Kelloggia brevipes
Heptapsogaster minutus
H. parvulus
Megaginus quadrithorax
Menacanthus laticephalus
Ornicolax alienus
O. mexicanus
O. robustus
Pseudolipeurus tinami
Pterocotes aberrans
Rhopaloceras simplex
Strongylocotes pellucidifrons
Little Tinamou, *Crypturellus soui*
Heptapsogaster costaricensis
H. tapicollae
Megaginus laticlypeus
Pectenosoma meserythra
Physconella kelloggi
Rhopaloceras rudimentarius
Slaty-breasted Tinamou, *Crypturellus boucardi*
Austrokelloggia boucardi
Discocorpus furculus
Heptapsogaster boucardi
H. modestae
H. tuxtlae
Megapeostus multiplex
Pectenosoma boucardi
Pseudolipeurus similis
Rhopaloceras heterogenitalis
Strongylocotes boucardi
Rufescent Tinamou, *Crypturellus cinnamomeus*
Heptapsogaster acutiventris
Heterogoniodes araeceps
Megapeostus secundus
Pectenosoma cinnamomea
Strongylocotes fimbriatus
S. interruptus
Bonaparte's Tinamou, *Nothocercus bonapartei*
Nothocotus distinctus
N. parvithorax

Common Loon, *Gavia immer*
Craspedonirmus bisetosus
Arctic Loon, *Gavia arctica*
Craspedonirmus atricolor
C. colymbinus
C. frontatus
Red-throated Loon, *Gavia stellata*
Craspedonirmus colymbinus
C. frontatus
Horned Grebe, *Podiceps auritus*
Aquanirmus colymbinus
Eared Grebe, *Podiceps caspicus*
Aquanirmus americanus
Incidifrons fulicae
Laemobothrion simili
Pseudomenopon insolens
Western Grebe, *Aechmophorus occidentalis*
Pseudomenopon par
Pied-billed Grebe, *Podilymbus podiceps*
Aquanirmus americanus
Short-tailed Albatross, *Diomedea albatrus*
Docophoroides brevis
D. pacificus
Harrisoniella densa
Perineus concinnus
P. giganticola
Procellariphaga navigans
P. pinquis
Black-footed Albatross, *Diomedea nigripes*
Docophoroides ferrisi
Episbates machilhennyi
Perineus confidens
Black-browed Albatross, *Diomedea melanophris*
Docophoroides harrisoni
D. murphyi
D. simplex
White-capped Albatross, *Diomedea cauta*
Docophoroides brevis
Yellow-nosed Albatross, *Diomedea chlororhynchos*
Docophoroides murphyi
Cape Petrel, *Daption capensis*
Ancistrona procellariae
Naubates testaceus
Procellariphaga daptionis
Pseudonirmus gurlti
Fulmar, *Fulmarus glacialis*
Ancistrona vagelli
Perineus nigrolimbatus
Austromenopon brevifimbriata
Saemundssonia occidentalis
Black-tailed Shearwater, *Adamastor cinereus*
Halipeurus agusticeps
Cory's Shearwater, *Puffinus diomedea*
Saemundssonia peusi
Pink-footed Shearwater, *Puffinus creatopus*
Naubates major
Greater Shearwater, *Puffinus gravis*
Halipeurus abnormis
Naubates harrisoni
Wedge-tailed Shearwater, *Puffinus pacificus*
Clypedon pacificus
Longimenopon puffinus
Sooty Shearwater, *Puffinus griseus*
Halipeurus diversus
Procellariphaga paulula
Manx Shearwater, *Puffinus puffinus*
Naubates major
Saemundssonia valida
Trabeculus aviator
T. miriabilis
Audubon's Shearwater, *Puffinus lherminieri*
Clypedon pacificus
Procellariphaga narboroughi
Fork-tailed Petrel, *Oceanodroma furcata*
Philoceanus annuliventris
Leach's Petrel, *Oceanodroma leucorhoa*
Acidoproctus kelloggi
Halipeurus subangusticeps
Saemundssonia incisa
Guadalupe Petrel, *Oceanodroma macrodactyla*
Longimenopon dominicanum
Red-billed Tropic-bird, *Phaëthon aethereus*
Austromenopon becki
Saemundssonia breviantennata
S. phaetona
Red-tailed Tropic-bird, *Phaëthon rubricauda*
Saemundssonia hexagona
White Pelican, *Pelecanus erythrorhynchos*
Colpocephalum unciferum
Piagetiella peralis
Brown Pelican, *Pelecanus occidentalis*
Colpocephalum unciferum
Pectinopygus occidentalis

Piagetiella bursaepelecani
Blue-faced Booby, *Sula dactylatra*
Pectinopygus jamaicensis
Blue-footed Booby, *Sula nebouxii*
Pectinopygus minor
Brown Booby, *Sula leucogaster*
Pectinopygus annulatus
P. garbei
Red-footed Booby, *Sula sula*
Pectinopygus sularum
Gannet, *Morus bassanus*
Eidmanniella pustulosa
Pectinopygus bassani
Great Cormorant, *Phalacrocorax carbo*
Eidmanniella brevipalpis
Pectinopygus gyricornis
Double-crested Cormorant, *Phalacrocorax auritus*
Eidmanniella kuwani
Pectinopygus gyricornis
Piagetiella incomposita
Olivaceous Cormorant, *Phalacrocorax olivaceus*
Eidmanniella eurygaster
Pectinopygus faralloni
P. gyroceras
Piagetiella vigua
Brandt's Cormorant, *Phalacrocorax penicillatus*
Eidmanniella kuwani
Piagetiella incomposita
Anhinga, *Anhinga anhinga*
Pectinopygus anhinge
Magnificent Frigate-bird, *Fregata magnificens*
Pectinopygus crenatus
Gray Heron, *Ardea cinerea*
Ardeicola ciconiae
A. ardeae
Ciconiphilus decimfasciatus
Common Egret, *Casmerodius albus*
Ardeicola albulus
Ciconiphilus obscurus
Little Egret, *Egretta garzetta*
Ardeicola expallidus
Black-crowned Night Heron, *Nycticorax nycticorax*
Ciconiphilus nyctardis
Least Bittern, *Ixobrychus exilis*
Ardeicola stellaris
American Bittern, *Botaurus lentiginosus*
Ardeicola stellaris
Wood Ibis, *Mycteria americana*
Ardeicola loculater
Ciconiphilus maculipes
C. femoratus
Colpocephalum scalariforme
Neophilopterus heteropygus
Glossy Ibis, *Plegadis falcinellus*
Ardeicola rhaphidius
Ciconiphilus blagoweschenskii
Colpocephalum leptopygos
Ibidoecus bisignatus
I. robustus
Plegadiphilus plegadis
White Ibis, *Eudocimus albus*
Colpocephalum fusconigrum
Ibidoecus bimaculatus
Scarlet Ibis, *Eudocimus ruber*
Ardeicola gracilentus
Ibidoecus hians
White Spoonbill, *Platalea leucorodia*
Eucolpocephalum femorale
Ibidoecus plataleae
Roseate Spoonbill, *Ajaia ajaja*
Colpocephalum ajajae
Ibidoecus iberoamericanus
American Flamingo, *Phoenicopterus ruber*
Anaticola candidus
Mute Swan, *Cygnus olor*
Ornithobius cygni
Whooper Swan, *Olor cygnus*
Anatoecus musicus
Whistling Swan, *Olor columbianus*
Ornithobius cygni
Canada Goose, *Branta canadensis*
Ornithobius goniopleurus
Trinoton anserium
Brant, *Branta bernicla*
Anaticola crassicornis
Anatoecus dentatus
Barnacle Goose, *Branta leucopsis*
Anatoecus brunneopygus
Ornithobius hexopthalmus
White-fronted Goose, *Anser albifrons*
Anaticola brevimaculatus
A. serratus
Trinoton squalidum

Domestic Goose, *Anser a. domesticus*
Anaticola anseris
Anatoecus adustus
Ciconiphilus parvus
C. pectiniventris
Ornithobius mathisi
Trinoton anserium
T. squalidum
Black-bellied Tree Duck, *Dendrocygna autumnalis*
Acidoproctus hopkinsi
Fulvous Tree Duck, *Dendrocygna bicolor*
Anaticola chaetodens
West Indian Tree Duck, *Dendrocygna arborea*
Acidoproctus maximus
White-faced Whistling Duck, *Dendrocygna viduata*
Acidoproctus rostratus
Sheld-Duck, *Tadorna tadorna*
Anaticola tadornae
Colpocephalum quadriseriatum
Mallard, *Anas platyrhynchos*
Anaticola crassicornis
A. parviceps
A. zukeri
Anatoecus adustus
Holomenopon transvaalense
Trinoton querquedulae
Black Duck, *Anas rubripes*
Anaticola crassicornis
Anatoecus dentatus
Trinoton lituratum
T. querquedulae
Gadwall, *Anas strepera*
Anaticola depurcatus
Anatoecus dentatus
Trinoton querquedulae
Pintail, *Anas acuta*
Holomenopon clypeilargum
Trinoton luridum
Common Teal, *Anas crecca*
Anaticola sordidus
Holomenopon leucoxanthum
Green-winged Teal, *Anas carolinensis*
Anatoecus dentatus
Blue-winged Teal, *Anas discors*
Anatoecus dentatus
European Widgeon, *Mareca penelope*
Anaticola penelopes
Holomenopon marecae
Trinoton spinosum
American Widgeon, *Mareca americana*
Anaticola crassicornis
Trinoton luridum
T. querquedulae
Shoveler, *Spatula clypeata*
Anaticola hopkinsi
Anatoecus ferrugineus
Holomenopon steigerum
Trinoton squalidum
Wood Duck, *Aix sponsa*
Anaticola lepidotus
Anatoecus dentatus
Redhead, *Aythya americana*
Anatoecus dentatus
Common Pochard, *Aythya ferina*
Anatoecus difficilis
Canvasback, *Aythya valisineria*
Acidoproctus kelloggi
Greater Scaup, *Aythya marila*
Anatoecus dentatus
Lesser Scaup, *Aythya affinis*
Anaticola cornicephalus
Anatoecus dentatus
Trinoton querquedulae
Tufted Duck, *Aythya fuligula*
Anatoecus obtusus
Barrow's Goldeneye, *Bucephala islandica*
Anaticola clangulae
Bufflehead, *Bucephala albeola*
Anaticola crassicornis
Anatoecus dentatus
Oldsquaw, *Clangula hyemalis*
Anaticola crassicornis
Anatoecus clangulus
A. natatorum
Common Eider, *Somateria mollissima*
Anaticola rubromaculatus
King Eider, *Somateria spectabilis*
Anatoecus dentatus
A. obtusus
Muscovy Duck, *Cairina moschata*
Anaticola cairinensis
A. zunkeri
Holomenopon cairinae
H. transvaalensis
Velvet Scoter, *Melanitta fusca*

Anaticola punctulatus
Anatoecus natatorum
Anaticus roesleri
White-winged Scoter, *Melanitta deglandi*
Anaticola constrictus
Holomenopon loomisi
Surf Scoter, *Melanittta perspicillata*
Anaticola constrictus
Common Scoter, *Oidemia nigra*
Anaticola augustolimbatus
Holomenopon lunarium
Trinoton minus
Ruddy Duck, *Oxyura jamaicensis*
Anaticola crassicornis
Hooded Merganser, *Lophodytes cucullatus*
Anatoecus dentatus
Common Merganser, *Mergus merganser*
Anaticola crassicornis
Anatoecus dentatus
A. ferrugineus
Trinoton querquedulae
Red-breasted Merganser, *Mergus serrator*
Anaticola crassicornis
A. mergiserrati
Anatoecus icterodes
Trinoton mergi
T. querquedulae
Turkey Vulture, *Cathartes aura*
Laemobothrion canalense
Colpocephalum kelloggi
Cuculiphilus alternatus
Falcolipeurus marginalis
Black Vulture, *Coragyps atratus*
Falcolipeurus marginalis
King Vulture, *Sarcoramphus papa*
Colpocephalum megalops
Cuculiphilus cathartaepapae
Falcolipeurus ternatus
Laemobothrion glutinans
White-tailed Kite, *Elanus leucurus*
Colpocephalum osborni
Hook-billed Kite, *Chondrohierax uncinatus*
Kurodaia keopeckei
Laemobothrion condrohieracis
Everglade Kite, *Rostrhamus sociabilis*
Craspedorrhynchus obscurus
Falcolipeurus quadriguttatus
Goshawk, *Accipiter gentilis*
Degeeriella secondaria
D. temporalis
Bicolored Hawk, *Accipiter bicolor*
Degeeriella epustulata
Cooper's Hawk, *Accipiter cooperii*
Craspedorrhynchus dilatatus
Degeeriella fusca
Red-tailed Hawk, *Buteo jamaicensis*
Colpocephalum napiforme
Craspedorrhynchus dilatatus
Laemobothrion loomisi
Red-shouldered Hawk, *Buteo lineatus*
Craspedorrhynchus buteonis
Broad-winged Hawk, *Buteo platypterus*
Kurodaia macrocybe
Swainson's Hawk, *Buteo swainsoni*
Colpocephalum costaricense
Laemobothrion buteonivorum
Rough-legged Hawk, *Buteo lagopus*
Craspedorrhynchus dilatatus
White Hawk, *Leucopternis albicollis*
Craspedorrhynchus candidus
Golden Eagle, *Aquila chrysaëtos*
Colpocephalum impressum
Craspedorrhynchus aquilinus
Degeeriella fulva
Falcolipeurus auturalis
Gray Sea Eagle, *Haliaeetus albicilla*
Colpocephalum flavescens
Craspedorrhynchus macrocephalus
Degeeriella discocephalus
Falcolipeurus sulcifrons
Bald Eagle, *Haliaeetus leucocephalus*
Craspedorrhynchus halieti
Degeeriella amblys
Marsh Hawk, *Circus cyaneus*
Degeeriella fusca
Osprey, *Pandion haliaetus*
Kurodaia haliaeti
Small Forest Hawk, *Micrastur ruficollis*
Craspedorrhynchus ultimus
C. transversifrons
Caracara, *Caracara cheriway*
Cuculicola splendidus
Guadalupe Caracara, *Caracara lutosus*
Degeeriella caracarensis
Gyrfalcon, *Falco rusticolus*
Degeeriella fasciata
Peregrine Falcon, *Falco peregrinus*
Degeeriella fusca

D. temporalis
Pigeon Hawk, *Falco columbarius*
Degeeriella temporalis
Kestrel, *Falco tinnunculus*
Degeeriella rufa
Laemobothrion tinnunculi
Rediella pediculoides
Sparrow Hawk, *Falco sparverius*
Degeeriella carruthi
D. castanea
D. giebeli
D. secondaria
Laemobothrion intermedium
L. loomisi
Curassow, *Crax rubra*
Oxylipeurus globicerus
Amyrsidea rubra
Crested Guan, *Penelope purpurascens*
Amyrsidea purpurascens
Oxylipeurus penelope
Chachalaca, *Ortalis vetula*
Amyrsidea spicula
Oxylipeurus vetulae
Dusky-headed Chachalaca, *Ortalis garrula*
Menacanthus ortalidis
Oxylipeurus costaricensis
O. postmarginatus
Black Chachalaca, *Penelopina nigra*
Chelopistes rotundus
Horned Guan, *Oreophasis derbianus*
Colpocephalum hoffmanni
Blue Grouse, *Dendragapus obscurus*
Goniodes simoni
G. merriamanus
Lagopoecus obscurus
Spruce Grouse, *Canachites canadensis*
Goniodes corpulentus
Ruffed Grouse, *Bonasa umbellus*
Goniodes bonasus
Lagopoecus umbellus
Willow Ptarmigan, *Lagopus lagopus*
Goniodes lagopi
Amyrsidea lagopi
A. striata
Lagopoecus affinis
Rock Ptarmigan, *Lagopus mutus*
Lagopoecus affinis
White-tailed Ptarmigan, *Lagopus leucurus*
Goniodes leucurus
Greater Prairie Chicken, *Tympanuchus cupido*
Goniodes cupido
Sharp-tailed Grouse, *Pedioecetes phasianellus*
Goniodes nebraskensis
Lagopoecus perplexus
Sage Grouse, *Centrocercus urophasianus*
Goniodes centrocerci
Lagopoecus gibsoni
Bobwhite, *Colinus virginianus*
Cuclotogaster maculipes
Goniodes ortygis
Lagopoecus numidianus
Lipeurus dovei
Oxylipeurus clavatus
O. cubanus
Black-throated Quail, *Colinus nigrogularis*
Oxylipeurus yucatensis
Scaled Quail, *Callipepla squamata*
Goniodes squamatus
Lagopoecus pallidus
Oxylipeurus callipeplus
California Quail, *Lophortyx californicus*
Goniodes mammilatus
G. ovoidalis
Lagopoecus docophoroids
Gambel's Quail, *Lophortyx gambelii*
Lagopoecus gambeli
Mountain Quail, *Oreortyx pictus*
Goniodes pictus
Lagopoecus californicus
Harlequin Quail, *Cyrtonyx montezumae*
Goniodes submamillatus
Lagopoecus mearnsi
Oxylipeurus montezumae
Ring-necked Pheasant, *Phasianus colchicus*
Amyrsidea megalosoma
Cuclotogaster heterographus
Goniocotes chrysocephalus
Goniodes capitatus
G. colchici
Lagopoecus colchicus
Lipeurus maculosus
Oxylipeurus colchicus
Gray Partridge, *Perdix perdix*
Amyrsidea megalosoma
A. perdicis
Cuclotogaster heterogrammicus

Goniocotes microthorax
G. simillimus
Goniodes dispar
Menopon pallens
Black-eared Wood-quail, *Odontophorus erythrops*
Chelopistes elongatus
C. heterurus
Oxylipeurus melanotus
Marbled Wood-quail, *Odontophorus gujanensis*
Oxylipeurus repandus
Spotted Wood-quail, *Odontophorus guttatus*
Oxylipeurus guttatus
White-throated Wood-quail, *Odontophorus leucolaemus*
Menacanthus meridionalis
Long-tailed Partridge, *Dendrortyx macroura*
Chelopistes simillis
Highland Partridge, *Dendrortyx leucophrys*
Chelopistes dendrortyx
Peacock, *Pavo cristatus*
Amyrsidea phaeostoma
Goniocotes parviceps
G. rectangulatus
Goniodes meinertzhageni
G. pavonis
Lipeurus pavo
Hen, *Gallus domesticus*
Cuclotogaster heterographus
Goniocotes gallinae
Goniodes assimilis
G. gigas
Lipeurus caponis
Menacanthus stramineus
Menapon gallinae
M. pallens
Guinea Hen, *Numida meleagris*
Goniocotes gallinae
Goniodes gigas
G. numidae
Lipeurus numidae
Menacanthus numidae
Menapon gallinae
Turkey, *Meleagris gallopavo*
Chelopistes meleagridis
Menacanthus stramineus
Oxylipeurus corpulentus
O. polytrapezius
Ocellated Turkey, *Agriocharis ocellata*
Oxylipeurus agriocharis
Whooping Crane, *Grus americana*
Heleonomus assimilis
Sandhill Crane, *Grus canadensis*
Gruimenopom canadense
Esthiopterum brevicephalus
Limpkin, *Aramus guarauna*
Ibidoecus scolopaceus
Laemobothrion cubense
Clapper Rail, *Rallus longirostris*
Rallicola californicus
Virginia Rail, *Rallus limicola*
Fulicoffula cumstocki
Incidifrons monachus
Rallicola californicus
Water Rail, *Rallus aquaticus*
Fulicoffula rallina
Incidifrons ralli
Pseudomenopon scopulacorne
Rallicola cuspidatus
Spotted Crake, *Porzana porzana*
Rallicola mystax
Yellow Rail, *Coturnicops noveboracensis*
Rallicola porzanae
Wood Rail, *Aramides cajanea*
Fulicoffula volsella
Rallicola ewingi
Mexican Crake, *Laterallus albigularis*
Fulicoffula obstinata
Pseudomenopon costaricense
Corn Crake, *Crex crex*
Rallicola ortygometrae
Purple Gallinule, *Porphyrula martinica*
Rallicola elliotti
Common Gallinule, *Gallinula chloropus*
Fulicoffula gallinula
Incidifrons gallinula
Laemobothrion chloropodis
European Coot, *Fulica atra*
Fulicoffula lurida
Incidifrons fulicae
Laemobothrion atrum
Pseudomenopon pilosum
Rallicola fulicae
American Coot, *Fulica americana*
Fulicoffula longipila
Incidifrons transpositus
Pseudomenopon pacificum

Rallicola fulicae
Sun Grebe, *Heliornis fulica*
Fulicoffula heliornis
Jacana, *Jacana spinosa*
Rallicola exiguifrons
European Oystercatcher, *Haematopus ostralegus*
Actornithophilus grandiceps
Austromenopon haemantopi
Saemundssonia haemantopi
American Oystercatcher, *Haematopus palliatus*
Lunaceps haemantopi
Quadraceps auratus
Lapwing, *Vanellus vanellus*
Actornithophilus svobodae
Lunaceps holophaeus
Saemundssonia temporalis
Ringed Plover, *Charadrius hiaticula*
Quadraceps fissus
Quadraceps hiaticulae
Saemundssonia platygaster
Semipalmated Plover, *Charadrius semipalmatus*
Quadraceps major
Q. opacus
Saemundssonia platygaster
Killdeer, *Charadrius vociferus*
Austromenopon aegialitidis
Quadraceps boephilus
Dotterel, *Eudromias morinellus*
Saemundssonia semivittata
American Golden Plover, *Pluvialis dominica*
Actornithophilus timidus
Quadraceps orarius
Saemundssonia hawaiiensis
Black-bellied Plover, *Squatarola squatarola*
Actornithophilus flavipes
Austromenopon squatarolae
Lunaceps incoenis
Quadraceps hospes
Saemundssonia naumanni
Ruddy Turnstone, *Arenaria interpres*
Rediellia pediculoides
Actornithophilus bicolor
Quadraceps strepsilaris
Black Turnstone, *Arenaria melanocephala*
Actornithophilus tigrus
American Woodcock, *Philohela minor*
Rhynonirmus infuscatus
European Woodcock, *Scolopax rusticola*
Austromenopon icterum
Cummingsiella aurea
Rhynonirmus helvolus
Common Snipe, *Capella gallinago*
Austromenopon durisetosum
Cummingsiella ambigua
Rhynonirmus scolopacis
Actornithophilus stictus
Rhynonirmus magnocephalus
European Jacksnipe, *Lymnocryptes minimus*
Actornithophilus multisetosus
Long-billed Curlew, *Numenius americanus*
Cummingsiella longirostricola
C. ovalis
Eurasian Curlew, *Numenius arquata*
Actornithophilus patellatus
Austromenopon crocatum
Cummingsiella ovalis
Lunaceps numenii
Saemundssonia humeralis
S. viridiscola
Whimbrel, *Numenius phaeopus*
Actornithophilus ocellatus
Austromenopon phaeopodis
Lunaceps phaeopi
Saemundssonia scolopacisphaeopodis
S. viridicola
Bristle-thighed Curlew, *Numenius tahitiensis*
Lunaceps hopkinsi
Eskimo Curlew, *Numenius borealis*
Lunaceps rileyi
Upland Plover, *Bartramia longicauda*
Rhynonirmus infuscatus
Spotted Sandpiper, *Actitis macularia*
Quadraceps ravus
Solitary Sandpiper, *Tringa solitaria*
Quadraceps waterstoni
Wood Sandpiper, *Tringa glareola*
Quadraceps obscurus
Wandering Tattler, *Heteroscelus incanum*
Actornithophilus kilauensis
Saemundssonia hawaiiensis
Polynesian Tattler, *Heteroscelus brevipes*
Quadraceps impar
Willet, *Catoptrophorus semipalmatus*

Austromenopon sachtlebeni
Quadraceps carrikeri
Greater Yellowlegs, *Totanus melanoleucus*
Quadraceps austini
Lesser Yellowlegs, *Totanus flavipes*
Quadraceps falcigerus
Knot, *Calidris canutus*
Lunaceps drosti
Saemundssonia canuti
S. islandica
Purple Sandpiper, *Erolia maritima*
Lunaceps nereis
Pectoral Sandpiper, *Erolia melanotos*
Actornithophilus morsitans
Least Sandpiper, *Erolia minutilla*
Actornithophilus morsitans
A. trilobatus
Carduiceps zonarius
Saemundssonia fusiformis
Dunlin, *Erolia alpina*
Austromenopon alpinum
Carduiceps meinertzhageni
C. zonarius
Short-billed Dowitcher, *Limnodromus griseus*
Actornithophilus albus
Long-billed Dowitcher, *Limnodromus scolopaceus*
Quadraceps klatti
Semipalmated Sandpiper, *Ereunetes pusillus*
Actornithophilus hirsutus
Western Sandpiper, *Ereunetes mauri*
Lunaceps cabanisi
Marbled Godwit, *Limosa fedoa*
Carduiceps clayae
Lunaceps clayae
L. lucidus
Rotundiceps cordatus
Bar-tailed Godwit, *Limosa lapponica*
Austromenopon meyeri
Carduiceps clayae
Saemundssonia limosae
Hudsonian Godwit, *Limosa haemastica*
Lunaceps paschalis
Rotundaceps cordatus
Black-tailed Godwit, *Limosa limosa*
Actornithophilus spimulosus
Austromenopon limosae
Carduiceps cingulatus
Saemundssonia tompsoni
Ruff, *Philomachus pugnax*
Actornithophilus pustulosus
Austromenopon lutescens
Carduiceps fulvofasciatus
Lunaceps holophaeus
Sanderling, *Crocethia alba*
Actornithophilus albus
Carduiceps complexivus
Lunaceps actophilus
American Avocet, *Recurvirostra americana*
Actornithophilus uniformis
Austromenopon indistinctum
Cirrophthirius recurvirostrae
C. testudinarius
Cummingsiella inexpectata
Quadraceps zephyra
Black-necked Stilt, *Himantopus mexicanus*
Actornithophilus mexicanus
Quadraceps mexicanus
Red Phalarope, *Phalaropus fulicarius*
Austromenopon corporosum
Quadraceps phalaropi
Wilson's Phalarope, *Steganopus tricolor*
Quadraceps fimbriatus
Northern Phalarope, *Lobipes lobatus*
Carduiceps subscalaris
Quadracepts connexus
Mexican Thick-knee, *Burhinus bistriatus*
Quadraceps acuticeps
Pomarine Jaeger, *Stercorarius pomarinus*
Actornithophilus brachycephalus
Austromenopon circinatum
A. fuscofasciatum
Perineus grandis
Perineus laculatus
Quadraceps stellaepolaris
Parasitic Jaeger, *Stercorarius parasiticus*
Quadraceps normifer
Saemundssonia cephalus
Long-tailed Jaeger, *Stercorarius longicaudus*
Quadraceps parvapallidus
Skua, *Catharacta skua*
Perineus piratae
Saemundssonia stresemanni
Glaucous Gull, *Larus hyperboreus*
Quadraceps striolatus
Saemundssonia lari
Glaucous-winged Gull, *Larus glaucescens*

Actornithophilus funebris
Austromenopon infrequens
Great Black-backed Gull, *Larus marinus*
Saemundssonia gonothorax
Actornithophilus lari
Herring Gull, *Larus argentatus*
Qudraceps ornatus
Ring-billed Gull, *Larus delawarensis*
Quadraceps sublingulatus
Mew Gull, *Larus canus*
Quadraceps ornatus
Saemundssonia congener
Black-headed Gull, *Larus ridibundus*
Austromenopon ridibundus
Quadraceps punctatus
Laughing Gull, *Larus atricilla*
Saemundssonia gonothorax
Bonaparte's Gull, *Larus philadelphia*
Actornithophilus funebris
Heermann's Gull, *Larus heermanni*
Quadraceps felix
Saemundssonia meinertzhageni
Ivory Gull, *Pagophila eburnea*
Saemundssonia pagophilae
Black-legged Kittiwake, *Rissa tridactyla*
Austromenopon transversum
Quadraceps lineolatus
Q. paulschulzei
Saemundssonia tridactylae
Ross' Gull, *Rhodostethia rosea*
Quadraceps bryki
Sabine's Gull, *Xema sabini*
Quadraceps lineatus
Forster's Tern, *Sterna forsteri*
Saemundssonia parvigenetalis
Common Tern, *Sterna hirundo*
Austromenopon pachypus
Quadraceps sellatus
Saemundssonia sternae
Arctic Tern, *Sterna paradisaea*
Quadraceps houri
Roseate Tern, *Sterna dougallii*
Quadraceps giebeli
Sooty Tern, *Sterna fuscata*
Quadraceps birostris
Q. lepidus
Q. obtusus
Saemundssonia peristicta
S. petersi
Bridled Tern, *Sterna anaethetus*
Saemundssonia meridiana
Royal Tern, *Thalasseus maximus*
Quadraceps praestans
Sandwich Tern, *Thalasseus sandvicensis*
Actornithophilus piceus
Saemundssonia laticaudata
Caspian Tern, *Hydroprogne caspia*
Quadraceps caspius
Q. griseus
Black Tern, *Chlidonias niger*
Actornithophilus maurus
Noddy Tern, *Anoüs stolidus*
Actornithophilus epiphanes
A. milleri
Clypedon incisus
Saemundssonia remota
Razorbill, *Alca torda*
Austramenopon nigropleurum
Quadraceps alcae
Saemundssonia celidoxa
Common Murre, *Uria aalge*
Austromenopon uriae
Quadraceps obliquus
Saemundssonia calva
Dovekie, *Plautus alle*
Austromenopon merguli
Quadraceps klatti
Saemundssonia merguli
Black Guillemot, *Cepphus grylle*
Saemundssonia grylle
Pigeon Guillemot, *Cepphus columba*
Quadraceps pacificus
Saemundssonia procax
Marbled Murrelet, *Brachyramphus marmoratum*
Saemundssonia montereyi
Ancient Murrelet, *Synthliboramphus antiquum*
Quadraceps maritimus
Saemundssonia montereyi
Cassin's Auklet, *Ptychoramphus aleutica*
Quadraceps maritimus
Saemundssonia isolita
S. montereyi
Crested Auklet, *Aethia cristatella*
Saemundssonia wumisuzume
Least Auklet, *Aethia pusilla*
Quadraceps aethereus

Rhinoceros Auklet, *Cerorhinca monocerata*
Quadraceps maritimus
Saemundssonia acutipecta
Common Puffin, *Fratercula arctica*
Austromenopon fraterculae
Saemundssonia fraterculae
Tufted Puffin, *Lunda cirrhata*
Actornithophilus perplanus
Quadraceps pacificus
Rock Dove, *Columba livia*
Campanulotes compar
Coloceras fahrenholzi
C. piageti
Colpocephalum turbinatum
Columbicola columbae
Horostiella lata
Mourning Dove, *Zenaidura macroura*
Columbicola baculoides
C. macrourae
Physconelloides zenaidurae
Passenger Pigeon, *Ectopistes migratorius*
Columbicola extinctus
Ground Dove, *Columbigallina passerina*
Columbicola passerinae
Mexican Parrotlet, *Forpus cyanopygius*
Paragoniocotes illustris
Psittacobrosus forpi
Red-and-Green Macaw, *Ara chloroptera*
Heteromenopon sincipitalis
Paragoniocotes mirabilis
Psittacomenopon acuticeps
Scarlet Macaw, *Ara macao*
Neopsittaconirmus trinoton
Paragoniocotes nanus
Green Macaw, *Ara militaris*
Epiara dimorpha
Yellow-billed Cuckoo, *Coccyzus americanus*
Cuculoecus coccygii
C. latifrons
Cuculiphilus decoratus
Black-billed Cuckoo, *Coccyzus erythropthalmus*
Cuculiphilus fasciatus
Squirrel Cuckoo, *Piaya cayana*
Cuculicola atopus
Smooth-billed Ani, *Crotophaga ani*
Osborniella crotophagae
Vernoniella guimaraesi
Groove-billed Ani, *Crotophaga sulcirostris*
Vernoniella macgregori
Barn Owl, *Tyto alba*
Kurodaia subpachygaster
Screech Owl, *Otus asio*
Kurodaia painei
Strigiphilus ceblebrachys
Great Horned Owl, *Bubo virginianus*
Strigiphilus oculatus
Snowy Owl, *Nyctea scandiaca*
Kurodaia menoponoides
Strigiphilus ceblebrachys
S. barbatus
Burrowing Owl, *Speotyto cunicularia*
Kurodaia pectinata
Strigiphilus speotyti
Great Gray Owl, *Strix nebulosa*
Strigiphilus remotus
S. syrnii
Long-eared Owl, *Asio otus*
Strigiphilus cursor
S. barbatus
Short-eared Owl, *Asio flammeus*
Strigiphilus cursor
S. nudipes
Squamulated Owl, *Ciccaba virgata*
Strigiphilus viridicus
Common Nighthawk, *Chordeiles minor*
Mulcticola macrocephalus
Chimney Swift, *Chaetura pelagica*
Dennyus dubius
Eureum ewingi
Vaux's Swift, *Chaetura vauxi*
Dennyus richmondi
Chestnut-collared Swift, *Chaetura rutila*
Dennyus brunneitorques
Spiny-tailed Swift, *Chaetura spinicauda*
Dennyus limbus
White-throated Swift, *Aëronautes saxatalis*
Dennyus bruneri
Smoky Swift, *Cypseloides fumigatus*
Dennyus spininotus
Black Swift, *Cypseloides niger*
Dennyus spiniger
Ruby-throated Hummingbird, *Archilochus colubris*
Ricinus lineatus
Costa's Hummingbird, *Calypte costae*
Trochiloecetes prominens
Anna's Hummingbird, *Calypte anna*

Bruelia eustigma
Rufous Hummingbird, *Selasphorus rufus*
Picicola snodgrassi
Trochiloecetes ochoterenai
Lesser Broad-tailed Hummingbird, *Selasphorus flammula*
Ricinus doratophorum
Rieffer's Hummingbird, *Amazilia tzacatl*
Ricinus jiminezi
Coppery-tailed Trogon, *Trogon elegans*
Trogonirmus eleganus
Large-tailed Trogon, *Trogon melanurus*
Trogonirmus melanurus
Violaceous Trogon, *Trogon violaceus*
Trogonirmus hastiformis
T. laticephalis
Belted Kingfisher, *Megaceryle alcyon*
Actornithophilus subpustulatus
Rufous-crowned Motmot, *Momotus mexicanus*
Philopterus dennyi
Blue-crowned Motmot, *Momotus momota*
Bruelia marginella
Emerald Toucanet, *Aulacorhynchus prasinus*
Austrophilopterus minutus
Collared Aracari, *Pteroglossus torquatus*
Austrophilopterus torquatus
Keel-billed Toucan, *Ramphastos sulfuratus*
Austrophilopterus subsimilis
Yellow-shafted Flicker, *Colaptes auratus*
Philopterus alienus
Picicola mississippiensis
Menacanthus colaptis
Penenirmus jugens
Pileated Woodpecker, *Dryocopus pileatus*
Picicola marginatulus
Gray-breasted Woodpecker, *Centurus hypopolius*
Menacanthus praecursor
Acorn Woodpecker, *Melanerpes formicivorus*
Penenirmus californiensis
Yellow-bellied Sapsucker, *Sphyrapicus varius*
Penenirmus californicus
P. varius
Hairy Woodpecker, *Dendrocopos villosus*
Penenirmus californiensis
Downy Woodpecker, *Dendrocopos pubescens*
Menopon hirsutum
Myrsidea funerea
Penenirmus evagens
Nuttall's Woodpecker, *Dendrocopos nuttallii*
Philopterus singularis
Black-backed Three-toed Woodpecker, *Picoïdes arcticus*
Menacanthus picicola
Northern Three-toed Woodpecker, *Picoïdes tridactylus*
Menacanthus picicola
Barred Antshrike, *Thamnophilus doliatus*
Machaerilaemus laticorpus
Masked Tityra, *Tityra semifasciata*
Machaerilaemus tityrus
White-collared Manakin, *Manacus candei*
Philopterus bruneri
Eastern Kingbird, *Tyrannus tyrannus*
Penenirmus tyrannus
Ricinus angulatus
Western Kingbird, *Tyrannus verticalis*
Picicola foedus
Cassin's Kingbird, *Tyrannus vociferans*
Ricinus arcuatus
Ash-throated Flycatcher, *Myiarchus cinerascens*
Menacanthus distinctus
Philopterus rufus
Picicola foedus
Say's Phoebe, *Sayornis saya*
Picicola foedus
Costa Rican Flycatcher, *Empidonax atriceps*
Myrsidea stenodesma
Western Flycatcher, *Empidonax difficilis*
Ricinus sucinaceus
Bruelia ductilis
Eastern Wood Pewee, *Contopus virens*
Philopterus fuscoventralis
Vermilion Flycatcher, *Pyrocephalus rubinus*
Philopterus insulicola
Skylark, *Alauda arvensis*
Menacanthus alaudae
Horned Lark, *Eremophila alpestris*
Ricinus serratus
Tree Swallow, *Iridoprocne bicolor*
Bruelia longa
Philopterus major

Bank Swallow, *Riparia riparia*
Bruelia tenuis
Myrsidea latifrons
Rough-winged Swallow, *Stelgidopteryx ruficollis*
Myrsidea pallorus
Barn Swallow, *Hirundo rustica*
Bruelia domestica
Machaerilaemus malleus
Myrsidea rustica
M. straminea
Purple Martin, *Progne subis*
Bruelia brevipes
Machaerilaemus americanus
Myrsidea dissimilis
Philopterus domesticus
Gray-breasted Martin, *Progne chalybea*
Dennyus similis
Blue Jay, *Cyanocitta cristata*
Philopterus cristata
White-tipped Brown Jay, *Psilorhinus mexicanus*
Philopterus underwoodi
Scrub Jay, *Aphelocoma coerulescens*
Menacanthus persignatus
Black-billed Magpie, *Pica pica*
Bruelia biocellata
Philopterus picae
Common Raven, *Corvus corax*
Bruelia argula
Menacanthus gonophaeus
Philopterus corvi
Common Crow, *Corvus brachyrhynchos*
Bruelia rotundata
Myrsidea interrupta
Philopterus corvi
Rook, *Corvus frugilegus*
Menacanthus laticeps
Philopterus atratus
Hooded Crow, *Corvus cornix*
Bruelia uncinosa
Piñon Jay, *Gymnorhinus cyanocephala*
Philopterus phillipi
Clark's Nutcracker, *Nucifraga columbiana*
Myrsidea brunea
Black-capped Chickadee, *Parus atricapillus*
Philopterus rutteri
Carolina Chickadee, *Parus carolinensis*
Bruelia vulgata
Verdin, *Auriparus flaviceps*
Bruelia audax
Common Bushtit, *Psaltriparus minimus*
Menacanthus robustus
Brown Creeper, *Certhia familiaris*
Penenirmus trimarginis
Dipper, *Cinclus mexicanus*
Menacanthus aleskensis
Philopterus americanus
Winter Wren, *Troglodytes troglodytes*
Penenirmus albiventris
Bewick's Wren, *Thryomanes bewickii*
Philopterus mirus
Cactus Wren, *Campylorhynchus brunneicapillum*
Menacanthus distinctus
Catbird, *Dumetella carolinensis*
Picicola orpheus
Red-wing, *Turdus musicus*
Bruelia iliaci
B. inornata
Myrsidea iliaci
Blackbird, *Turdus merula*
Bruelia ansel
B. jacobi
B. merulensis
Philopterus merulae
Ricinus ernstlangi
Clay-colored Robin, *Turdus grayi*
Penenirmus caligineus
Robin, *Turdus migratorius*
Bruelia vulgata
Ricinus merulae
Sturnidoecus simplex
Fieldfare, *Turdus pilaris*
Bruelia antimarginalis
Philopterus bischoffi
Wood Thrush, *Hylocichla mustelina*
Myrsidea incerta
Hermit Thrush, *Hylocichla guttata*
Myrsidea incerta
Swainson's Thrush, *Hylocichla ustulata*
Myrsidea incerta
Gray-cheeked Thrush, *Hylocichla minima*
Myrsidea incerta
Veery, *Hylocichla fuscescens*
Myrsidea fuscomarginata
Eastern Bluebird, *Sialia sialis*
Philopterus sialii

Golden-crowned Kinglet, *Regulus satrapa*
Ricinus frenatus
White Wagtail, *Motacilla alba*
Menacanthus pusillus
Philopterus passerinus
Sturnidoecus aeneas
Yellow Wagtail, *Motacilla flava*
Philopterus passerinus
Water Pipit, *Anthus spinoletta*
Ricinus japonicus
Meadow Pipit, *Anthus pratensis*
Bruelia cordyalla
Bohemian Waxwing, *Bombycilla garrula*
Bruelia brachythorax
Philopterus garrulae
Ricinus bombycillae
Cedar Waxwing, *Bombycilla cedrorum*
Bruelia cedrorum
Phainopepla, *Phainopepla nitens*
Bruelia peninsularis
Picicola foedus
Northern Shrike, *Lanius excubitor*
Bruelia imponderabilica
Menacanthus camelinus
Starling, *Sturnus vulgaris*
Bruelia nebulosa
Menacanthus mutabilis
Myrsidea cucularis
Sturnidoecus sturni
Crested Myna, *Acridotheres cristatellus*
Myrsidea invadens
Prothonotary Warbler, *Protonotaria critrea*
Ricinus pallens
Blue-winged Warbler, *Vermivora pinus*
Ricinus picturatus
Orange-crowned Warbler, *Vermivora celata*
Ricinus picturatus
Yellow Warbler, *Dendroica petechia*
Myrsidea ridulosa
Yellow-breasted Chat, *Icteria virens*
Picicola foedus
House Sparrow, *Passer domesticus*
Bruelia obligata
B. subtilis
B. vulgata
Menacanthus annulatus
Philopterus fringillae
European Tree Sparrow, *Passer montanus*
Bruelia cyclothorax
B. subtilus
Wagler Oropendola, *Zarhynchus wagleri*
Bizarrifrons francisi
Myrsidea luoris
M. miriabilis
Bobolink, *Dolichonyx oryzivorus*
Menacanthus expansus
Eastern Meadowlark, *Sturnella magna*
Bruelia abrupta
B. picturata
Yellow-headed Blackbird, *Xanthocephalus xanthocephalus*
Bruelia xanthocephali
Redwinged Blackbird, *Agelaius phoeniceus*
Bruelia ornatissima
Philopterus agelaii
Scarlet-headed Oriole, *Icterus pustulatus*
Machaerilaemus icterus
Boat-tailed Grackle, *Cassidix mexicanus*
Bizarrifrons meinertzhageni
Common Grackle, *Quiscalus quiscula*
Philopterus quiscali
Brown-headed Cowbird, *Molothrus ater*
Bruelia ornatissima
Swainson Tanager, *Piranga bidentata*
Bruelia melanococa
Cardinal, *Richmondena cardinalis*
Menacanthus spinosus
Rose-breasted Grosbeak, *Pheucticus ludovicianus*
Bruelia pallidula
Varied Bunting, *Passerina versicolor*
Ricinus australis
Dickcissel, *Spiza americana*
Myrsidea incerta
Brambling, *Fringilla montifringilla*
Bruelia cyclothorax
Evening Grosbeak, *Hesperiphona vespertina*
Bruelia pallidula
Purple Finch, *Carpodacus purpureus*
Bruelia vulgata
House Finch, *Carpodacus mexicanus*
Bruelia vulgata
Myrsidea conspicua
Pine Grosbeak, *Pinicola enucleator*
Menacanthus alaskensis
Chestnut-capped Atlapetes, *Atlapetes brunnei-nucha*
Menacanthus difficilis

European Goldfinch, *Carduelis carduelis*
Bruelia densilimba
Menacanthus carduelis
American Goldfinch, *Spinus tristis*
Myrsidea incerta
Red Crossbill, *Loxia curvirostra*
Bruelia limbata
Myrsidea quadrimaculata
Philopterus curvirostrae
Rufous-sided Towhee, *Pipilo erythrophthalmus*
Bruelia vulgata
Myrsidea melanorum
Ricinus subhastatus
Brown Towhee, *Pipilo fuscus*
Bruelia vulgata
Savannah Sparrow, *Passerculus sandwichensis*
Ricinus diffusus
Lark Sparrow, *Chondestes grammacus*
Bruelia augustifrons
Sage Sparrow, *Amphispiza belli*
Bruelia lautiuscula
White-winged Junco, *Junco aikeni*
Ricinus hastatus
R. pallidus
Slate-colored Junco, *Junco hyemalis*
Bruelia vulgata
Ricinus pallidus
Oregon Junco, *Junco oreganus*
Penenirmus mirinotatus
Ricinus hastatus
R. pallidus
Tree Sparrow, *Spizella arborea*
Bruelia vulgata
Field Sparrow, *Spizella pusilla*
Machaerilaemus complexus
White-crowned Sparrow, *Zonotrichia leucophrys*
Bruelia vulgata
Golden-crowned Sparrow, *Zonotrichia atricapilla*
Bruelia vulgata
Fox Sparrow, *Passerella iliaca*
Ricinus angulatus
Song Sparrow, *Melospiza melodia*
Ricinus melospizae
Machaerilaemus maestus
M. melospizae
Menacanthus chrysophaeus
Lapland Longspur, *Calcarius lapponicus*
Bruelia infrequens
Menacanthus meniscus
Snow Bunting, *Plectrophenax nivalis*
Bruelia nivalis
Myrsidea major
Philopterus hamatus
Ricinus angulatus

DEPARTMENT OF BIOLOGY, CENTRAL MICHIGAN UNIVERSITY, MT. PLEASANT, MICHIGAN, OCTOBER 3, 1959

GENERAL NOTES

Flight distance in the Great Blue Heron.—Flight distance, as defined by Hediger (1950. "Wild Animals in Captivity," p. 32), is that distance at which an animal will take flight when approached by a supposed enemy. Flushing distance means the same. While Hediger recognizes variation between species, within species, and among individuals of a species, he maintains that a definite, specific flight distance exists within fixed limits.

Measurement of flight distance depends on two basic factors: (1) it must be possible to see the animal at distances greater than the outer limit and (2) reasonable evidence must exist to indicate that the animal is aware of the approaching object before the outer limit is reached. The Great Blue Heron (*Ardea herodias*) is a species which is large enough to be seen from considerable distances, and it usually exhibits head movements which give evidence of an awareness of approach. For example, birds which are fishing will have the head tilted downward; when disturbed the head is moved to a more horizontal position, after which the flight reaction occurs if approach is continued.

Observations were made on flight distance of the Great Blue Herons at Lake Itasca, Minnesota, during the period June 25 to July 12, 1957. The principal aim of the study was to determine the limits of flight distance for this species. Another objective was to determine whether variation of flight distance within the limits could be related to such factors as speed of approach and elevation of birds with reference to water level.

Observations were made from a rowboat equipped with an outboard motor. Herons at the shore line were located from open water with the aid of binoculars. An approach run was made on each bird by steering directly toward it on a line perpendicular to the shore line. During the last part of each run a rangefinder was used to determine boat-to-bird distance at the moment of flight.

Most of the approach runs were made using oars. Rowing was held to a constant speed and every attempt was made to limit unnecessary motion. Other runs were made with the 12-horsepower motor set at slow, medium or fast speed. The majority of birds approached were standing in or near the water and were apparently feeding, but some were perched on trees at heights up to 40 feet. Whenever it was possible to see the new location of a bird after flushing, the boat was returned to open water and another approach was made. This procedure was repeated on each bird as often as possible in order to collect data on the flight distance of specific individuals.

Flight distances ranged from 13 to 166 yards, indicating a considerable amount of variability. In fact, it seemed doubtful that flight distance had any promise as a quantitative basis for the study of behavior of the Great Blue Heron if these observations were a valid representation of the fixed limits for the species. However, it was apparent that some observations were of doubtful validity. Flight distances greater than 140 yards were more than three standard deviations from the mean, which may indicate that some birds were exhibiting the flight reaction in relation to factors other than the approach of the boat. Even the smallest values may have occasionally been in error, since preoccupation with other factors might have permitted closer than normal approach. One heron, which was being harrassed by two Redwinged Blackbirds (*Agelaius phoeniceus*), did not fly until the boat was within 10 yards. That the detection of the approach was late seemed supported by the fact that the heron was in an awkward position and did not successfully initiate flight on the first attempt because of inadequate preparatory motions.

An increase of flight distance was indicated by mean values obtained on four successive sampling dates. Table 1 contains this information, with data confined to approaches made at rowing speed toward birds less than 10 feet above the water. It was impossible to guess whether the increase, if real, was related to seasonal factors or to repeated

testing. There was no way of knowing whether the same birds were being observed on the different dates.

Speed of approach made no apparent difference in mean flight distance of birds near water level. However, an increase did occur in relation to birds at positions 10 or more feet above water. At every speed except rowing, increased height was related to greater mean values for flight distance, and apparently was effective in aiding birds to detect increased speed. From this it would appear that increased confidence did not accompany movement to greater heights, but that height did increase perception, possibly in connection with advantage of angle.

All comparisons of mean flight distance were considered tenuous because possible differences were cancelled out by variance within each sampling condition. Unless variability could be assigned to some factor or combination of factors, the use of flight distance as a quantitative basis for further investigation of the behavior of this species did not seem valid.

An indication of one source of variability was obtained from those measurements made by successive approaches on the same subject. During the study period, 25 subjects were approached at least twice in succession. Some estimate of the nature of variability for individuals was possible from the fact that the average range for flight distance was 40 feet. Seven of the 25 birds did not vary at all from one approach to the next. A standard analysis of variance indicated that differences between individuals were significant (1 per cent level). This could be taken as evidence that variation of flight

TABLE 1

FLIGHT DISTANCE IN YARDS UNDER VARIOUS CONDITIONS

Date	Boat Speed	Elevation of Bird	Number of Observations	Mean Distance	Distance Range	S.D.
June 25	rowing	0	5	24	23– 33	5.5
June 26	rowing	0	14	35	23– 66	17.5
June 29	rowing	0	47	44	16– 66	15.9
July 12	rowing	0	5	63	25–166	22.9
	rowing	low*	79	42	16–166	21.9
		high*	48	40	13–100	19.9
	slow motor	low	28	47	20–100	24.0
		high	20	62	15–133	37.3
	medium motor	low	2	41	30– 50	—
		high	11	73	41–100	23.6
	fast motor	low	6	47	33– 60	20.2
		high	2	58	33– 83	—

*low is less than 3 yards; high is 3 or more yards.

distance for individuals was less than first thought, and further that much of the variability noted during the study was due to differences between individuals. It follows that any future work should be confined to birds individually marked for recognition.

These observations were made while the authors were attending the Lake Itasca Forestry and Biological Field Station with the support of the National Science Foundation.
—HOWARD D. ORR, *St. Olaf College*, AND THEODORE W. SUDIA, *University of Minnesota*, *March 27, 1959.*

Polygyny and other notes on the Redwinged Blackbird.—These observations were made on a one-acre cattail marsh at Itasca State Park, Minnesota, from June 19 to July 16, 1958, in connection with my studies at the University of Minnesota Biological Station. The somewhat isolated marsh is located in the southeast corner of the crossroads of Route 92 and the north boundary road of the park. Dr. John T. Emlen, Jr. found four Redwinged Blackbird (*Agelaius phoeniceus*) nests on June 19. Nests A, B and C contained young birds and Nest D was almost completed. Nests A, C and D were in a triangle almost in the center of the marsh and about 25 feet from each other. Nest B was almost 100 feet south of the southernmost nest in the triangle. I observed the nests 27 times with each visit lasting from ½ to 3½ hours and distributed through the day from 4:30 a.m. to 10:00 p.m.

In his studies of the Redwinged Blackbird in Wisconsin, Nero (1956. *Wilson Bull.*, 68: 35) states that "polygyny was common, but no more than three females were ever observed with one male; two was average." The population of unbanded adults in the area which I studied consisted of a single male with a bald white spot on his forehead and four females, one with an unusually light face, two with almost identical markings, and a fourth with half of her tail feathers much shorter than the others. I found, as did Nero, that the females were "out of phase" in their breeding cycles; the young left the nests on June 23, 27, 30, and July 15, at Nests A, B, C, and D, respectively.

I observed that the adults fed and gathered food for the young only outside the nesting area, usually in the marsh across the north boundary road. The male did not help feed the young; each female fed her own brood until the young from Nest C were destroyed two days after fledging. During the next 10 days on 12 occasions I saw both Females B and C feeding the two fledglings from Nest B, and this entire group left the marsh on the same day.

The resident male defended his territory by "song spread," "bill tilting," and attack, when necessary, from male Redwinged Blackbirds (apparently unmated and immature birds who sometimes entered the area) as well as from a pair of Baltimore Orioles (*Icterus galbula*) nesting nearby. When one of these intruders entered the territory, the resident male first gave a warning call, which sent the females into the willow trees to the south of the nests, and then he chased away the intruder. On one occasion when two males (one immature) were being chased away, one of the females flew into view and perched on a cattail. Immediately the resident male abandoned his pursuit of the intruders and chased her back to the willows. The area was not defended against other nesting species including a Ruby-throated Hummingbird (*Archilochus colubris*) and two Yellowthroats (*Geothylpis trichas*). Once when a Red-tailed Hawk (*Buteo jamaicensis*) circled high over the area the male displayed, gave an alarmed call, exposed his epaulets, and flew over the territory. Nero (*op. cit.*: 125–130) found that "nearly all Redwings on the marsh sat quietly on their perches with concealed epaulets when hawks were soaring overhead." Each female defended a small area around her nest, particularly against other females. On three occasions I saw the females band together and chase an immature male from the territory.

With three exceptions the observations of this brief study corresponded closely with those of Nero. A single male appeared to have a harem of four females, all with nests from which young fledged. On at least 12 occasions over a ten-day period two unbanded but easily identified females fed the fledglings from a single nest after one of these females had just lost her entire fledged brood. When a Red-tailed Hawk appeared over the area, the male made himself conspicuous.—Ruth Strosnider, *Woodrow Wilson High School, Washington, D. C., April 27, 1959.*

A record of swimming in Bobwhites.—Twenty-eight Bobwhites (*Colinus virginianus*) were observed to swim between 600–700 feet, approximately one-half the distance across the main axis of the west portion of 3300-acre Lake Carl Blackwell, Payne County, Oklahoma on October 13, 1958. The birds were seen about 7 a.m. slightly south of a point mid-distance from either shore where a north-south transect across the lake measured almost 500 yards. The quail were scattered in an area 10x40 feet swimming toward the south shore. The water was glassy calm, otherwise the birds probably would have gone unnoticed.

The head, neck and upper third of the body were all that protruded above the water as the Bobwhites "paddled" slowly along until 18 reached the south shore line. These individuals appeared completely exhausted. The remaining 10 birds, one of which was only 2 feet from shore, floated quietly just holding their heads above water. These floating birds offered no resistance when picked up by hand and placed in the grass at the shoreline. Two quail were so fatigued that they could not stand, but fell on their side when placed in the grass.

Two days later one dead bird was found intact where it had been placed in the grass, and the remains of two others had been partially eaten by some predator.

It is possible that these birds were attempting to fly across the lake, although the 500 yards is not an extreme distance for quail to fly. The birds could have been flushed some distance from the shore line and then become exhausted attempting to fly across the lake. This seems unlikely since the quail were able to swim the 600- to 700-foot distance and should have been able to fly the same distance more easily. Although there was no fog in the area where the Bobwhites were first seen, approximately 20 minutes earlier in another portion of the lake a light fog rising from the water surface was evident. With a light fog and perfectly calm water, the birds could have alighted in the lake by accident.

A weekly news report of the Oklahoma Wildlife Conservation Department dated November 7, 1958, gave another account of six quail being rescued from Ft. Gibson Reservoir in Northeastern Oklahoma. Population pressures may have some bearing on these unusual incidents. High Bobwhite populations in Oklahoma during the fall of 1958 produced many unusual behavior and distribution patterns. Coveys of quail were reported in downtown areas in several cities and quail were seen regularly in residential sections from late summer throughout the fall period.—WILLIAM R. HEARD, *Department of Zoology,* (Contribution No. 288) *Oklahoma State University, May 18, 1959.*

Ground nest of Florida Red-shouldered Hawk.—On Saturday, March 7, 1959, I visited the area of the Kissimmee Prairie between Lake Jackson and Lake Kissimmee, Florida. Having visited this area many times since 1950 I knew where several birds usually nested. For this reason a search was made through a small cabbage palm hammock on the west side of Lake Jackson, in Osceola County, for a nest of a Red-shouldered Hawk (*Buteo lineatus*). A single bird was seen on the outside, and upon entering this hammock a nest was found that had been blown to the ground by the recent high winds. Some 40 yards away another such nest was found. Both of these nests were composed of Spanish moss, oak sticks, shreds of airplant, and a few pieces of oak twigs with green leaves still attached.

After walking another few yards, possibly 20, I heard a scream from a bird flying overhead through the treetops. I immediately started looking closely in the trees for the new nest, as the parent bird remained close by and continued to call. Soon a nest with two warm eggs was found on the ground about 9 feet from the base of an oak and entirely unconcealed.

The nest was composed of Spanish moss, a branch of oak twig with green leaves, two pieces of coarse brown fiber from the cabbage palm and a piece of green plant commonly known as "dog fennel." This nest resembled the lining portion of most tree nests, but lacked the sticks and twigs.

The parent bird made several passes overhead and uttered the usual scream as she did so.

Some eight years previous a frail nest with two broken eggs was found in this same hammock. An investigation revealed this nest had been built on a horizontal palm frond, some 7 feet above the ground, and had blown off the night before.

This appears to be the only record of ground nesting of the Red-shouldered Hawk.—CHARLES E. CARTER, *1339 30th Street, Orlando, Florida, June 8, 1959.*

ORNITHOLOGICAL NEWS

In accordance with a decision of the 13th International Congress of Zoology, 1948, public notice is hereby given of the possible use by the International Commission on Zoological Nomenclature of its plenary powers in connection with the following case, full details of which will be found in *Bulletin of Zoological Nomenclature*, Vol. 17, Parts 6/8, to be published on April 8, 1960:

Suppression of the generic name *Drepanis* Brisson, 1760 (Class Aves). Z. N. (S)901.

Anyone who wishes to comment on this change should do so in writing, and in duplicate, as soon as possible, and in any case before October 8, 1960. Each comment should bear the reference number. Comments received early enough will be published in the *Bulletin of Zoological Nomenclature*. Those received too late for publication will, if received before October 8, 1960, be brought to the attention of the Commission at the time of commencement of voting.

Communications should be addressed as follows:

The Secretary,
International Commission on Zoological Nomenclature,
c/o British Museum (Natural History),
Cromwell Road,
London, S.W. 7.,
England.

The American Museum of Natural History, New York 24, New York, announces that a post-doctoral Fellowship for one year will be available in its Department of Birds, beginning on October 1, 1960. Inquiries may be directed to the Chairman, Department of Birds.

In "Water Birds of Penobscot Bay," distributed at the Rockland meeting of the Wilson Ornithological Society in June, 1959, appears on page 14 the statement under Eider that "over 100 well-grown young and over 300 nests were observed." Actually, we found over 100 nests and saw over 300 well-grown young. Unfortunately the transposition of the figures was not caught in the proofreading.—*Frederick V. Hebard.*

Mrs. Harriet Buchheister, wife of Carl W. Buchheister, President of the National Audubon Society, has an appeal that she hopes will bring help from readers of *The Wilson Bulletin*. For several years she has been working with crippled or blind and otherwise handicapped children and has been bringing joy and instruction into their lives by letting them learn birds by handling bird skins and mounted specimens. Unfortunately, the specimens wear out and need to be renewed occasionally. Will all those who collect and have extra specimens—either prepared skins or mounted ones—please send them to Mrs. Buchheister at 1239 Madison Avenue, New York City, New York. If new fresh skins or mounts are made, she asks you to please use borax instead of arsenic in their preparation and indicate same.—*John K. Terres.*

ORNITHOLOGICAL LITERATURE

THE BIRDS. By Oskar Heinroth and Katharina Heinroth. Translated by Michael Cullen. University of Michigan Press, Ann Arbor, 1958: 5¼x8⅛ in., 181 pp., 91 figs. $5.00. (First published in 1955 as Aus dem Leben der Vogel, second enlarged edition, by Springer-Verlag, Berlin-Goettingen-Heidelberg.)

A conventional review of this unusual book would be an injustice. To be sure there is a table of contents listing titles of the 22 chapters, and there is an index. But the chapter titles are inconsistent in style and their meaning is not always clear. They range from "The Nest" (Chapter 2) and "Color and Pigment" (15) to "Keeping Clean" (16) and "Getting About" (20). There is little or no balance among subject matter in the chapters, while certain specific subjects (for example, eggs) are discussed in widely scattered sections of the book. The length of the chapters varies greatly. Chapter 9, which is peculiarly titled "Is the Size of a Bird Related to the Size of Its Egg?" has the total length of one printed page. The index is limited to only the common names of species and groups of species, followed by their scientific names in parentheses and by page numbers.

These comments about an ordinary book would constitute a major criticism, but this is not an ordinary book. What, then has it? The first and truly intriguing aspect is the series of illustrations, each of which has a real purpose. Although they are small, their clarity of reproduction is exceptional. A few are line drawings, but most are photographs of nests, eggs, young, and adults, some showing special anatomical details. The purpose of all of the illustrations has been excellently achieved. They show us what birds really look like and, in many instances, why they behave as they do. An outstanding example are the neatly posed side and front views of a featherless Vasa Parrot which perfectly demonstrate the actual shape of a bird's body.

The illustrations serve to stimulate an interest in the text, which proves to be readable, smoothly flowing, and informative. It would be incorrect to say that this book is a complete work on ornithology, but it is nonetheless a complete story in itself, one that the reader may not easily leave unfinished. There is in it that rare quality of sensitivity to special details about living birds and that personal touch of the gifted authors, Dr. and Mrs. Heinroth. Dr. Heinroth was an ornithologist who knew birds so well that he could write of them as distinct personalities. We are fortunate to have their book made available to us in this very fine translation.—DWAIN W. WARNER.

BIRDS OF MARTHA'S VINEYARD WITH AN ANNOTATED CHECK LIST. By Ludlow Griscom and Guy Emerson. Privately printed, 1959: 5½x8¼ in., xiv+164 pp., 1 map. $4.50. (For sale at National Audubon Society, 1130 Fifth Ave., New York 28, N. Y.; Massachusetts Audubon Society, 155 Newbury St., Boston 16, Mass.; and Avery's, Edgartown, Martha's Vineyard, Mass.)

This attractive, handsomely printed little volume resulted from the collaboration of at least ten persons. The senior author, the late Ludlow Griscom, originally prepared the annotated list of bird species; Mrs. Ruth P. Emery revised and brought it up to date to include records as recently as 1957. The final list of 342 species comprises the bulk of the book. Annotations on each species usually consist of a statement of status, followed by dates when reported, sometimes localities where seen, and the last names (no initials) of observers. For full names of observers the reader may consult a list in the back pages of the book. In a few instances, where there is more than one observer with the same

last name, the reader has no way of knowing to which observer he is being referred. The annotations rarely include data on ecology (or even habitats), nests, and breeding habits. An excellent feature of the book is a summary or digest of the annotated list. This consists of six so-called Seasonal Lists to one of which each of the 342 species is assigned. On the line beside the name of the species is a brief designation of status. Altogether the lists provide a convenient device for quick reference.

What could have been a very useful feature of the book, "Where to Find Birds in Martha's Vineyard," is most disappointing. Despite the large, tipped-in, folding map, adequately detailed as to places and routes, the accompanying text of two pages is so imprecise as to be useless. Though it mentions some of the places on the map, it fails to state exactly how one reaches them and what he may expect when he gets there.

The book is concluded by a list of references to literature and a good index to bird species by both common and technical names.—Olin Sewall Pettingill, Jr.

Lead Poisoning as a Mortality Factor in Waterfowl Populations. By Frank C. Bellrose. Illinois Natural History Survey Bulletin, Vol. 27, Article 3, May, 1959: pp. 235–288; 31 tables, 9 figs. (2 charts, 7 photos), frontis. photo.

This paper reports extensive field and laboratory analysis of the incidence and effects of lead poisoning in waterfowl, between 1938 and 1955. Principal emphasis is on the Mallard and the Mississippi Flyway, but 23 species and all flyways are considered and compared. A complete review of reported die-offs is followed by detailed sections on the availability of lead, ingested lead shot in migrating fall and winter ducks, and effects of lead in wild Mallards dosed and released. Four pages of critical discussions and three pages of concise summary make the voluminous and important information in this bulletin readily available. Bellrose estimates the annual loss due to lead poisoning at 4 per cent for Mallards in the Mississippi Flyway and between 2 and 3 per cent for the total waterfowl population in North America, but thinks that the damage is not yet severe enough to warrant drastic regulations. The incidence of poisoning and the numbers of waterfowl hunters are both currently on the increase, posing a new management problem for the not-distant future.—T. L. Quay.

Food Habits of Migrating Ducks in Illinois. By Harry G. Anderson. Illinois Natural History Survey Bulletin, Vol. 27, Article 4, August, 1959: pp. 289–344; 43 tables, 18 figs. (15 photos, 2 charts, 1 map), frontis. photo.

The long and excellent series of research papers on waterfowl biology from the Illinois Natural History Survey is continued in the present bulletin. A total of 4977 duck gizzards of 17 species was collected in the autumns of 1938, 1939, and 1940 from hunters along the Illinois (90.5 per cent) and Mississippi rivers. The food contents were identified and calculated in minute detail, by the percentage volume method. The sample by species was roughly proportional to the estimated numbers in the fall flight, the seven commonest species and number of gizzards being: Mallard—2825, Pintail—881, Lesser Scaup—220, Blue-winged Teal—129, Green-winged Teal—393, Baldpate—160, and Ring-necked Duck—120. The foods and feeding habits of each species, including seasonal changes between October 16 and December 15, are presented in separate tables and discussions. The plant food items are listed in the tables by species only. Generic totals would have facilitated comparative understanding, since the genus is commonly used as the significant level in food habits literature. The ecology, availability, and use of each of the 19 most important plant species are discussed, and 12 of them figured. Animal foods amounted to only 5.52 per cent of the total organic contents, and the percentage volumes of many of the items

in the tables carried to the rather meaningless level of four decimal places. The summary is too short to do full justice to the included data. Anderson is to be congratulated for publishing at this time this useful information which he collected 20 years ago, rather than leaving it in the files forever.—T. L. QUAY.

THE BIRDS OF THE SASKATCHEWAN RIVER, CARLTON TO CUMBERLAND. By C. Stuart Houston and Maurice G. Street. Special Pub. No. 2, Saskatchewan Natural History Society, Regina, Saskatchewan, 1959: paper covered, 5½x8½ in., 205 pp., 4 maps, illus. $1.50.

This volume is an excellent example of the valuable contributions which amateurs can make to scientific ornithology. The senior author is a physician, as were so many outstanding naturalists of an earlier period. Undoubtedly the precise training for such a profession imbues an individual with the idea that accuracy of observing and reporting is essential. This is not always realized by many amateurs. That a professional education is not essential, however, is illustrated by the work of the junior author whose education was limited to that taught in the local schools. Not only are his observations accurate but they are remarkable in the fact that he commenced his diary of bird migration at the age of 12.

The book deals with a narrow area in the eastern half of Saskatchewan, along the rivers of the same name, from Carlton, 200 miles northeast to Cumberland House. Here the parkland of the Transition Zone merges with evergreen forests of the Canadian Zone. The region is too far north to attract a number of prairie forms. Black Ducks and Wood Ducks have occasionally occurred. The Eastern Kingbird is a common summer resident, but the Western Kingbird has been reported but twice.

Nipawin and Prince Albert may be strange names but every taxonomist and student of nomenclature will be familiar with Carlton and Cumberland House. The latter, established by Samuel Hearne in 1774, is the oldest community in Saskatchewan. The senior author has written brief sketches of these four regions and biographies of Hearne (1745–1792), John Richardson (1787–1867) and Thomas Drummond (1790–1835) who served under Sir John Franklin, Blakeston (1832–1891), Eugene Bourgeau (1815–1887) and R. R. MacFarlane (1833–1920), as well as those of his contemporaries. A bibliography of 144 titles will prove invaluable to future students of this area.

Based upon these earlier records and the observations of the authors, Houston has collected records for 259 species and seven considered hypothetical. For each he reviews the historical status and adds an ample account of their present status in the region concerned. Among these are five species for which the area is the type locality: Forster's Tern, Olive-sided Flycatcher, Gray-crowned Rosy Finch, Clay-colored Sparrow and Smith's Longspur. From an obscure botanical article, he discovered that Forster's Tern was actually collected by Drummond "some 10 to 50 miles upriver from Cumberland House" and not downstream, possibly in Manitoba, as suggested in the 5th edition of the A. O. U. Check-list. We learn that "Carlton specimens constitute the first known records to science of Swainson's Hawk" and that Nipawin is possibly the site where Henry Kelsey on July 24, 1691, shot three Passenger Pigeons, the earliest records for Western Canada.

A casual reader might assume that the work of the senior author overshadowed that of his associate. This is far from true. To appreciate the contribution of Street, one must have worked in the Canadian Zone to realize the difficulties he encountered in his studies of the status of the breeding birds. He has found or checked the nests of 131 species, and the flightless young of 10 more, in a 20-mile radius of Nipawin. Can

such a record be equalled? His findings include 33 nests of the Gray Jay, 20 of the Red-breasted Nuthatch, and the parasitization of 29 species by the Brown-headed Cowbird! Breeding ranges given in the 5th A. O. U. Check-list are extended by his nesting records for the Goshawk, Northern Three-toed Woodpecker, Gray Jay, House Wren, Catbird, Swainson's Thrush, Veery, Mountain Bluebird, Solitary, Philadelphia and Warbling Vireos and the Orange-crowned Warbler.

The authors are to be congratulated for the excellency of this volume which is remarkably free from errors. The Saskatchewan Natural History Society should be commended for making the information available at such a moderate price.—A. E. Allin.

Wildlife Conservation. By Ira N. Gabrielson. Second edition. The Macmillan Company, New York, 1959: 5½x8½ in., 244 pp., 23 maps and diagrams, 32 black and white plates. $5.50.

The first half of this book is an elementary treatment of the interrelations of natural resources; succeeding chapters on Grassland Conservation, Migratory Birds, Refuges, and Surmounting the Obstacles to Conservation, though brief, will interest more advanced students. The 16-page Grasslands chapter is the most dynamic one in the book, especially in its treatment of the pronghorn antelope. More discussion of the effects of present government agricultural policy would have made it unique as a brief statement of the major problem we face in bringing sound management to an area equal to two-fifths of the land area of the United States.

As one would expect of its author, there are many valuable insights into the problems discussed. On page 117, Dr. Gabrielson transcends his profession by stating flatly that the task we face is one of repairing the damage caused by past abuses, to "put natural constructive processes back to work." And in a brief discussion of crop-destruction by birds, he reminds us that it is the effect of this damage on the "margin of profit," rather than the proportion of the total crop affected, that makes this problem so difficult.

But the attempt to separate all topics according to popular interest in them results in chapters that mention nearly everything but almost never in such juxtaposition as to stimulate interest or excite concern. Conservation, as a doctrine, was born of conflict of interest, but there is little controversy here, no politics; instead, almost every paragraph suffers from over-qualification.

One almost wishes that Dr. Gabrielson had shunned this revisionary stint and addressed himself to a critical analysis of existing trends in wildlife conservation, a task few Americans are so well qualified to do. In this book he seems too often to have worked in an editorial straight-jacket.—Roland C. Clement.

A Field Guide to Bird Songs arranged to accompany Roger Tory Peterson's "A Field Guide to the Birds." Houghton Mifflin Company, Boston, 1959. $10.00.

This adjunct to Peterson's "A Field Guide to the Birds" is a comprehensive and systematic collection of recordings of the songs and calls of 305 species of North American birds found east of the Rocky Mountains. The recordings have been placed on both sides of two 12-inch long-playing records (with six to eight separate bands on each side) and arranged to accompany, page-by-page, the most recent edition of Peterson's Guide. The recordings were made in the field by the Laboratory of Ornithology, Cornell University, under the direction of Dr. Peter Paul Kellogg and Dr. Arthur A. Allen. Credit is given to 27 individuals who contributed one or more recordings or assisted in other ways.

The total playing time is approximately 80 minutes, nearly equally divided between non-passerines and passerines. Each species receives about 4 to 28 seconds of playing time and is introduced very briefly by Arthur Allen who gives the bird's name and corresponding page in Peterson's Guide. Almost every bird voice is carefully edited and beautifully clear.

Here, at a very reasonable price, is another precision tool to facilitate field identification of birds. Included are the songs and calls of 18 ducks and geese, 15 falconiform birds, 4 alcids, 10 woodpeckers including the Ivory-billed, 8 vireos, 30 warblers, 43 fringillids, and so on. One hears the voice of a Kirtland's Warbler in Michigan, a colony of Gannets in Quebec, and a clear "honk" of a Canada Goose in New York State. In many cases a quick and easy comparison of the voices of related species can be made, as with Black-capped, Carolina, and Brown-capped Chickadees. However, the compactness of the recordings makes it nearly impossible to make an immediate comparison of such species as the Yellow-throated and the Red-eyed Vireos without picking up the Blue-headed and Black-whiskered Vireos in between.

The two records are contained in an attractive, sturdy, book-like jacket. Printed inside is a list of the species, arranged in playing sequence and marked according to the side of the record and number of the band. Thus, it is easy to find the approximate location of a given species on the records.

As described by Peterson in an oral introduction to the records, an effort was made to select the most typical song or call of the species. I believe this has been accomplished. Almost all of the recordings are of very high quality, clear and precise. With very few exceptions, background noise is at a minimum. One marvels at the labor and technical achievement of accumulating the songs and calls of a high percentage of the birds of eastern and central North America and placing them in a carefully edited sequence on two records. An extreme case of the painstaking effort involved is 28 seconds of Red-winged Blackbird calls put together from 5 states and one Canadian province. For other species, such as some of the warblers and sparrows with simple songs, there are only two to four songs in a matter of four to ten seconds before the next species is introduced. To those accustomed to listening to much longer intervals per species as on most bird records, the short intervals for the songs and the speed in passing from bird to bird may be somewhat distracting at first, but after a little practice in listening, the short intervals usually prove entirely adequate and efficient. However, in a very few cases, the time allowed is definitely too brief. For instance, the two "mews" from the Redhead are not enough; one needs more than the two calls of the Red-headed Woodpecker; and the whistle of the wings of the Common Goldeneye is cut off too short. Also, the Pine Grosbeak is almost inaudible.

Every member of the growing army of serious bird watchers should have a copy of "A Field Guide to Bird Songs." However, grade school children, high school students and older beginners should not start with it, but rather with bird call records which emphasize fewer birds taken more slowly. On the other hand, all high schools should have "A Field Guide to Bird Songs" available for those students who develop an active interest in birds. College ornithology classes will find it a tremendous asset. An advance copy was used in the ornithology course at the University of Michigan Biological Station last summer, and proved to be an excellent teaching medium. It is reported that the students nearly wore it out.—NICHOLAS L. CUTHBERT.

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Manuscripts intended for publication in *The Wilson Bulletin* should be neatly typewritten, double-spaced, and on one side only of good quality white paper. Tables should be typed on separate sheets. Before preparing these, carefully consider whether the material is best presented in tabular form. Where the value of quantitative data can be enhanced by use of appropriate statistical methods, these should be used. Follow the A. O. U. Check-list (Fifth Edition, 1957) insofar as scientific names of United States and Canadian birds are concerned unless a satisfactory explanation is offered for doing otherwise. Use species names (binomials) unless specimens have actually been handled and subspecifically identified. Summaries of major papers should be brief but quotable. Where fewer than five papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited. Photographs for illustrations should be sharp, have good contrast, and be on glossy paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Authors are requested to return proof promptly. Extensive alterations in copy after the type has been set must be charged to the author.

A Word to Members

Th Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

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If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Merrill Wood, Dept. of Zoology and Entomology, Frear Laboratory, Pennsylvania State University, University Park, Pennsylvania. He will notify the printer.

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Lynds Jones, 1890–1893
Willard N. Clute, 1894
R. M. Strong, 1894–1901
Lynds Jones, 1902–1908
F. L. Burns, 1909–1911
W. E. Saunders, 1912–1913
T. C. Stephens, 1914–1916
W. F. Henninger, 1917
Myron H. Swenk, 1918–1919
R. M. Strong, 1920–1921
Thos. L. Hankinson, 1922–1923
Albert F. Ganier, 1924–1926
Lynds Jones, 1927–1929
J. W. Stack, 1930–1931
J. M. Shaver, 1932–1934
Josselyn Van Tyne, 1935–1937
Margaret Morse Nice, 1938–1939
Lawrence E. Hicks, 1940–1941
George Miksch Sutton, 1942–1943
S. Charles Kendeigh, 1943–1945
George Miksch Sutton, 1946–1947
Olin Sewall Pettingill, Jr., 1948–1950
Maurice Brooks, 1950–1952
W. J. Breckenridge, 1952–1954
Burt L. Monroe, 1954–1956
John T. Emlen, Jr., 1956–1958
Lawrence H. Walkinshaw, 1958–1960